

EVOLUTION: STILL A THEORY IN CRISIS



MICHAEL DENTON

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Description

More than thirty years after his landmark book *Evolution: A Theory in Crisis* (1985), biologist Michael Denton revisits his earlier thesis about the inability of Darwinian evolution to explain the history of life. He argues that there remains “an irresistible consilience of evidence for rejecting Darwinian cumulative selection as the major driving force of evolution.” From the origin of life to the origin of human language, the great divisions in the natural order are still as profound as ever, and they are still unsupported by the series of adaptive transitional forms predicted by Darwin. In addition, Denton makes a provocative new argument about the pervasiveness of nonadaptive order throughout biology, order that cannot be explained by the Darwinian mechanism.

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Praise for *Evolution: Still a Theory in Crisis*

“Of all the books that have been critical of Darwinian evolution in recent years, Michael Denton’s *Evolution: Still a Theory in Crisis* stands out for doing more than simply compiling the full range of evidence—from cosmology through all of biology to the origins of human language—that goes against a blind, incrementalist view of the development of life. To be sure, Denton does that very well. But the book’s real triumph is to frame this criticism in terms of an alternative paradigm, one indebted to Darwin’s great rival Richard Owen. This proposed new paradigm is founded on the idea of discrete biological forms, or ‘types,’ which have the standing of natural laws. Denton is consistently clear and scrupulous about how the evidence bears on neo-Darwinism vis-à-vis what might be called his ‘neo-Owenism.’ All told, *Evolution* is the one book that I would recommend to any student or lay person who wants to think in positive, scientific terms out of Darwin’s black box.”

Steve Fuller, Auguste Comte Professor of Social
Epistemology, University of Warwick, UK, and author
of *Science vs. Religion?* and *Dissent over Descent*

“Darwinists often deflect trenchant criticisms by kicking the can down the road. In ten or twenty years science will surely show their theory is correct, they say. Now thirty years after his groundbreaking book, *Evolution: A Theory in Crisis*, Michael Denton calls their bluff. Not only hasn’t Darwinism overcome its challenges, severe new problems have made the crisis much worse.”

Michael Behe, PhD, Professor of Biological Sciences, Lehigh University, and author of *Darwin’s Black Box* and *The Edge of Evolution*

“Based on a great variety of indisputable facts from biology and paleontology, Michael Denton presents in his new book a highly competent and very thoughtful critique of the neo-Darwinian paradigm. His arguments convincingly suggest that modern biology prematurely dispensed with the notions of typology, essentialism, structuralism, and laws of biological form as promising alternative approaches to the origin of biological complexity and diversity. His affirmation of common descent with modification also demonstrates that well-founded doubts concerning the capabilities of the neo-Darwinian mechanism cannot be easily dismissed as anti-evolution propaganda, but should rather be welcomed even by neo-Darwinists as heuristically fruitful.”

Günter Bechly, PhD, Paleontologist

“In this book Michael Denton moves adroitly from the history of ideas to scientific explanation. *Evolution: Still a Theory in Crisis* is really two books in one: an insightful and fearless historical analysis on the one hand, and a provocative manifesto for a ‘new’ biology on the other. It is a rare and powerful combination that demands careful reading.”

Michael A. Flannery, Professor and Assistant Dean for Special
and Historical Collections, University of Alabama at Birmingham,
and author of *Alfred Russel Wallace: A Rediscovered Life*

“Biologist Michael Denton has written a devastating critique of Darwinian evolution. Denton is not a creationist, but a structuralist. He makes a compelling argument, supported by abundant evidence, that the most basic structures of living things—their forms or body

plans—are not adaptive and cannot be explained by the cumulative selection that is at the core of evolutionary theory. Instead, he argues, those forms are part of the very fabric of nature. Everyone involved in the controversies over evolution should read this book.”

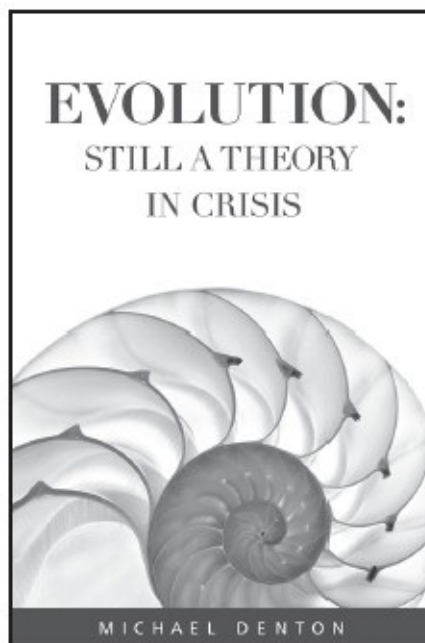
Jonathan Wells, PhD, Biologist and Senior Fellow, Discovery Institute,
and author of *Icons of Evolution* and *The Myth of Junk DNA*

“Michael Denton’s new book *Evolution: Still a Theory in Crisis* is a substantial reworking of his classic book of (nearly) the same name. In this new book, he expands his argument against Darwinian adaptation as a mechanism capable of explaining the patterns we see in life. Using his considerable knowledge of historical and modern biology, he makes a fresh and compelling argument about the origins of animal form that will be completely new to many readers. I urge anyone interested in these questions to read this book.”

Ann Gauger, PhD, Senior Research Scientist, Biologic
Institute, and co-author of *Science and Human Origins*

Learn More about the Work of Michael Denton

You can access more information about Michael Denton, reviews of his new book, and a series of video conversations with him at the book’s website.



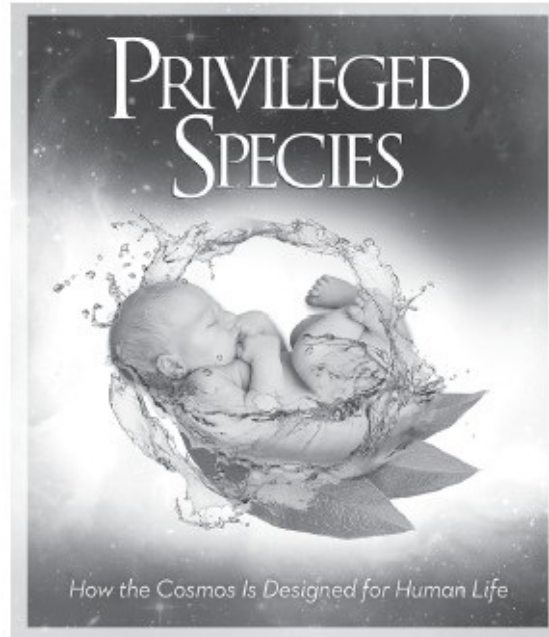
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The Biology of the Baroque

“The Biology of the Baroque” is a documentary featuring Michael Denton that explores the mystery of non-adaptive order in nature, order that cannot be explained by Darwinian evolution.

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1. Introduction

All in all, the empirical pattern of... nature conforms remarkably well to the typological model. The basic typological axioms—that classes are absolutely distinct, that classes possess unique diagnostic characters, that these diagnostic characteristics are present in fundamentally invariant form in all members of a class—apply almost universally throughout the entire realm of life.

Michael Denton, *Evolution: A Theory in Crisis* (1985), 117.

My main aim in *Evolution: A Theory in Crisis* (1985) was to argue that nature is fundamentally discontinuous. As I pointed out, the major taxa-defining characteristics, such as hair in the case of mammals or feathers in the case of birds, are not led up to from putative ancestral forms via long series of functional intermediates (which I termed “continuums of functional forms”¹). Moreover, they have remained invariant in all of the very diverse members of the groups they define.² I argued that the absence of such functional continuums poses an existential threat to classical Darwinian adaptive gradualism and the claim that macroevolution is no more than an extension of microevolution. I defended vigorously the notion that factors beyond cumulative selection must have shaped the course of evolution. Altogether, *Evolution* was a “full frontal” critique of the standard Darwinian model. It implied that the natural system is a natural discontinuum rather than the functional continuum that Darwinian biologists claim.

I argued that the taxa are analogous to distinct geometric figures such as triangles or quadrilaterals, which cannot be approached via little successive steps from some other class of geometric figure.³ I thereby defended the typological view that the taxa or Types are ontologically real and distinct components of the world order, as was widely believed in the nineteenth century before Darwin. This was the view D’Arcy Wentworth Thompson defended in his classic *On Growth and Form*:

Nature proceeds *from one type to another* among organic as well as inorganic forms; and these types vary according to their own parameters, and are defined by physico-mathematical conditions of possibility. In natural history Cuvier’s “types” may not be perfectly chosen nor numerous enough, but *types* they are; and to seek for stepping-stones across the gaps between is to seek in vain, for ever.⁴

I still adhere to this discontinuous typological view, although since I wrote *Evolution*, I have adopted a much more structuralist conception of organic order and particularly of the Types. When I wrote *Evolution*, I was a convinced pan-adaptationist and held to a strictly functionalist view of biological systems. I saw adaptation as the major or sole organizing principle of life, and I regarded organisms as primarily “adaptive bundles,” analogous to machines like a watch, in which every feature is there to serve some specific adaptive end. I saw the Types primarily as a limited set of highly integrated functional wholes—“Cuvierian Types” as referred to in the above quotation—highly constrained for functional reasons, like a complex machine, against even slight degrees of evolutionary change.⁵

But I failed to see what is very obvious to me now, more than thirty years later, as a convinced structuralist: While “Cuvierian functional constraints” may well play a role in “isolating the Types,”⁵ not all features of living things are there to serve some adaptive purpose, and many of the taxa-defining novelties—such as the pentadactyl limb (Tetrapoda) or the concentric whorls of the flower (angiosperms)—give every appearance of being a-functional “primal patterns” which have never served any specific adaptive end. Such apparently non-adaptive forms pose, as Richard Owen showed in his landmark publication *On the Nature of Limbs*⁷ (ten years before Darwin’s *Origin*), a self-evident challenge to pan-adaptationism. Indeed, these apparently non-adaptive forms pose an existential threat to the whole Darwinian and functionalist paradigm, because they imply that causal factors other than cumulative selection to serve functional ends *must* have played a crucial role in shaping living systems.

At the outset, I need to define two terms I will use frequently throughout the rest of the book. One is the term “homolog.” As I use it, this term refers to a unique biological characteristic or trait shared by all the members of a particular group such as the pentadactyl ground plan of the tetrapod limb shared by all tetrapods. A homolog is therefore a “taxa-defining novelty.” The term homolog is used frequently by researchers in evolutionary developmental biology (evo-devo) to describe such character traits.⁸ Systematists often describe homologs as “synapomorphies” or “apomorphies”⁹ In the nineteenth century, Richard Owen termed them “primal patterns.”¹⁰

The other word I need to define is “non-adaptive,” which I also employ throughout the book. I use this term to refer to any feature or characteristic of an organism which does not appear to serve any conceivable *specific* adaptive end—in other words, any feature that makes no contribution to the fitness of the organism. Such features are invisible to natural selection because natural selection only sees traits which serve some adaptive end. Examples might be the shape of a maple leaf (a non-adaptive feature restricted to an individual species of plant) or the pentadactyl limb (an example shared by many thousands of different vertebrate species).

My major goal in this new book is to review the challenge to Darwinian orthodoxy and the support for typology provided by the novelty and extraordinary invariance of the homologs. In addition, I will explore how the adaptive status of many homologs is clearly in doubt.

1.1 Structuralism and Functionalism

For two centuries, biologists have adhered to two opposing conceptions regarding the fundamental nature of organic form, one referred to as structuralism (or formalism) and the other as functionalism.¹¹ These two diametrically opposed conceptions of organic order were referred to by Stephen Jay Gould in his magisterial *The Structure of Evolutionary Theory*:

Most organisms are well adapted to their immediate environments [conditions of existence], but also built on anatomical ground plans that transcend any particular circumstance. Yet the two principles [functionalism or structuralism] seem opposed in a curious sense—for why should structures adapted for particular ends root their basic structure in homologies that do not now express

any common function (as in Darwin's example of mammalian forelimbs)?

The designation of one principle or the other as the causal foundation of biology virtually defines the position of any scientist towards the organic world and its causes of order... Shall we regard the plan of high-level taxonomic order as primary, with local adaptation viewed as a set of minor wrinkles... upon an abstract majesty? Or do local adaptations build the entire system from the bottom up? This dichotomy set the major debate of pre-Darwinian biology.¹²

a. Structuralism

According to the structuralist paradigm, a significant fraction of the order of life and of every organism is the result of basic internal constraints or causal factors that arise out of the fundamental physical properties of biological systems and biomatter. In other words, biological order that does *not* result from adaptation to satisfy functional ends. One of the simplest examples of this kind of order, “structural order,” is the cell membrane, which organizes itself into a thin layer covering the surface of the cell due entirely to the hydrophobic character of its lipid components—i.e., due to physical law—irrespective of any functional end it may serve.

These internal constraints, or “laws of biological form” as they were referred to in the nineteenth century,¹³ were believed by many biologists before Darwin to limit the way organisms are built to a few basic designs or Types, just as the laws of chemical form or crystal form limit chemicals and crystals to finite sets of lawful forms. This view implies that many of life's basic forms arise in the same way as do other natural forms—ultimately from the self-organization of matter—and are *genuine universals*. Structuralism—at least in the form it took in the nineteenth century, and in the version I am defending here—implies that the basic Types of life, and indeed the whole evolutionary progression of life on earth, are built into nature. Thus, life is no artifact of “time and chance,” as it came to be seen after Darwin, but a predictable and necessary part of the cosmic whole.



Figure 1-1. Richard Owen. Drawn in 1850.

For Richard Owen, the father of Anglo-Saxon structuralism, the idea that life on earth is the result of a lawful natural process was explicitly affirmed in the concluding chapter of his *Anatomy of Vertebrates*, where he claimed that the path of evolution was “preordained... due to innate capacity or power of change, by which nomogenously-created [generated by law] protozoa have risen to the higher forms of plants and animals.”¹⁴ As E. S. Russell showed in his classic *Form and Function*, nearly every early

nineteenth-century pre-Darwinian biologist—including such luminaries as Karl Ernst von Baer, Étienne Geoffroy, Isidore St. Hilaire, Henri Milne-Edwards, Étienne Serres, Johann Friedrich Meckel, Carl Gustave Carus, Heinrich Georg Bronn, and Theodore Schwann—believed life’s overall order to be the result of *lawful*, if unidentified, processes: the celebrated but “elusive laws of form.”¹⁵

As I commented in a previous article:

Given the lawful *Zeitgeist* of pre-Darwinian biology and given the enigmatic *abstract nature* of so many of the homologies and their *invariance* in so many diverse kinds of organisms through such vast periods of time it was a small inferential step to view them as changeless natural forms analogous to crystals or atoms. Geoffroy, perhaps the leading continental formalist, assumed the homologies to have “powers” analogous to atoms and other unalterable elements of the physical world... Owen also used the crystal analogy unambiguously in the final chapter of his *Anatomy of Vertebrates*, in the context of a discussion of the causes of segmentation: “The repetition of similar segments in a vertebral column and of similar elements in a vertebral segment, is analogous to the repetition of similar crystals.” The metaphor was also used by Theodore Schwann, the co-founder of the cell theory. In the last chapter of his *Microscopical Researches* he draws extensive parallels between cells and crystals:

The process of crystallization in inorganic nature... is... the nearest analogue to the formation of cells... Should we not then be justified in putting forward the proposition that the formation of the elementary parts of organisms is nothing but a crystallization... and the organism nothing but an aggregate of such crystals?... If a number of crystals capable of imbibition are formed, they must combine according to certain laws so as to form a systematic whole, similar to an organism.

The metaphor was used extensively by [Ernst] Haeckel who, echoing Schwann, talks of “cells as organic crystals, of crystal trees, of the analogy between assimilation by the cell and the growth of crystals in a mother liquid.”¹⁶

Consistent with the notion that the homologs or “primal patterns” are natural forms and genuine *universals* which should occur throughout the universe wherever there is life, Owen speculated in the closing section of *Limbs* about the possibility of the vertebrate homolog or *Bauplan* being actualized on other planets.¹⁷

Günter Wagner, in his recent book *Homology, Genes, and Evolutionary Innovation*, describes Owen’s structuralist view thus:

[Owen] thought that it should be possible to describe the organization of an animal body in the form of a body “formula” just like the composition of a chemical can be written in the form of a chemical formula. For example, H_2SO_4 is just a configuration of “chemical elements” (H, S and O) and their molecular proportions combined into a molecule (i.e., sulphuric acid).

For Owen, the analogues of chemical elements are the homologs in biology; that is, homologs are the anatomical “atoms” of the bodies that, in

different combinations and configurations, make up the various specific bodies of actual animals.¹⁸

As I explained in my previously quoted article:

Structuralists adhere... to a strictly “non-selectionist, non-historicist” view of the biological world. Leading 20th-century structuralists include the inventor of the term ‘genetics,’ William Bateson, D’Arcy Wentworth Thompson, author of the classic structuralist work *On Growth and Form*, Rupert Riedl, Stuart Kauffman, Brian Goodman, and Stuart Newman.

Although Gould was, as he himself confesses, a convinced pan-selectionist in his early years, he was increasingly sympathetic to structuralism in his later years. In *The Structure of Evolutionary Theory* he writes: “I don’t see how anyone could read, from Goethe and Geoffroy down through Severtzov, Remane and Riedl, without developing some appreciation for the plausibility, or at least the sheer intellectual power, of morphological explanations outside the domain of Darwinian functionalism.”¹⁹

Of course, all structuralists accepted that organisms exhibited adaptations to serve external environmental conditions. But these were considered to be, as Owen described them, “adaptive masks,” grafted as it were onto underlying ground plans or “primal patterns.” Thus the great diversity of vertebrate limbs—fins for swimming, hands for grasping, wings for flying—are all modifications of the same underlying ground plan or primal pattern, which serves no particular environmental necessity. As Gould puts it in the quote cited earlier, they “transcend any particular circumstance.”

Owen saw the “primal patterns” to be generated during development by what he called the “polarizing force,” while the adaptive masks were the result of another fundamental mechanism he termed the “adaptive force.”²⁰ As I cautioned in an earlier paper:

It is important to stress that structuralism... implies that organic order is a *mixture of two completely different types of order, generated by two different causal mechanisms*: a primal order... [including the taxa-defining homologs] generated by natural law, and a secondary adaptive order imposed by environmental constraints (by natural selection according to Darwinists, by Lamarckian mechanisms and by intelligent design according to current design theorists). The adaptive order of living things [which serves specific immediate environmental constraints] represents *a completely different sort of order, outside of the explanatory framework of structuralism altogether*. This means that structuralism per se can never give a complete causal explanation for all organic order. Structuralism is NOT a biological theory of everything.²¹

The origin of the natural laws that generate the primal order is, of course, its own important question. As I and others have argued elsewhere, those laws may point to the intelligent design of the universe as uniquely fit for life.²² But arguing that thesis is not the purpose of this book.

b. Functionalism

According to the opposing paradigm, often referred to as functionalism, the main or sole fundamental organizing principle of biology is adaptation. On this view, the main Type-defining homologs (pentadactyl limb, etc.) are adaptations built by cumulative selection during the course of evolution to serve various adaptive ends. Biological order built in this way is contingent in the sense that it is *undetermined by natural law*. Functionalists reject the structuralist notion that there is a significant amount of biological order that is the result of physical law, i.e., immanent in nature or arising from intrinsic constraints inherent in biological systems or the properties of biomatter. According to the functionalist view, organisms are, in essence, like machines, contingent assemblages of functional parts arranged to serve particular adaptive ends.²³ This is, of course, the currently prevailing and mainstream view. All Darwinists, and hence the great majority of evolutionary biologists, are *functionalist by definition*, as all evolution according to classical Darwinism comes about from cumulative selection to serve functional ends.

It is hard to imagine two scientific frameworks as diametrically opposed as structuralism and functionalism. Where functionalism suggests that *function* is prior and determines structure, structuralism suggests that *structure* is prior and constrains function. It is extraordinary to think that leading biologists have seen exactly the same empirical facts as pointing in such very different directions. As Russell stresses in *Form and Function*:

The contrast between the teleological attitude, with its insistence upon the priority of function to structure, and the morphological attitude, with its conviction of the priority of structure to function, is one of the most fundamental in biology.

Cuvier and Geoffroy are the greatest representatives of these opposing views. Which of them is right? Is there nothing more in the unity and diversity of organic forms than the results of functional adaptation, or is Geoffroy right in insisting upon an element of unity which cannot be explained in terms of adaptation?²⁴

Intriguingly, English natural theology from the seventeenth century²⁵ right up to the mid-nineteenth century also adhered strictly to an extreme form of pan-adaptationism, affirming that all the order of a living organism is adaptive and there to serve some immediate purpose—even male nipples, as John Ray claimed!²⁶ This is why the machine analogy famously associated with William Paley—organisms as “watch-like” purposeful assemblages of adaptive components—has been popular with creationists no less than with Darwinists.²⁷ Of course, creationists both before and after Darwin see adaptation as the result of the Divine watchmaker, while Darwin and subsequent Darwinists see it as the result of the “blind watchmaker,” cumulative selection.

The English-speaking world has adhered to some version of functionalism for so long (creationists since the seventeenth century and Darwinists since 1859) that it is inconceivable to most English-speaking biologists that living things might contain a significant degree of order arising from basic internal physical constraints rather than from adaptive processes. Consequently, there is no doubt that the structuralist claim—that the biological realm is undergirded by ground plans which serve no specific adaptive purpose—is alien to English-speaking biology.

1.2 The Neo-Darwinian Synthesis

Back in the mid-1980s, while I was preparing the final drafts of *Evolution*, the so-called modern synthesis or neo-Darwinian synthesis—a virulently functionalist worldview—was still the predominant paradigm among evolutionary biologists. The synthesis had arisen four to five decades earlier out of the work of a handful of key mid-century evolutionary biologists (geneticists Ronald Fisher, J. B. S. Haldane and Sewall Wright, biologists Ernst Mayr and Julian Huxley, and paleontologist Gaylord Simpson), and it was aimed at providing an exclusively functionalist evolutionary framework.²⁸ The makers of the synthesis desired to show that all evolutionary change—not just at the microevolutionary level—could be accounted for by the cumulative selection of small adaptive changes. In other words, macroevolution is a mere extension of microevolution. By returning to a strictly functionalist and externalist evolutionary model, the makers of the synthesis hoped to banish, once and for all, non-Darwinian notions of causation from evolutionary biology.²⁹ Thus, all other interpretations of evolution were rendered anachronistic and suspect. These included the structuralist views of Richard Owen and many pre-Darwinian biologists,³⁰ the ideas of D’Arcy Thompson,³¹ orthogenetic³² and vitalist³³ notions, Lamarckian theories,³⁴ and other internalist notions which had been popular during the first quarter of the twentieth century.

Consequently, the emphasis on adaptation from the 1950s to the 1970s and 1980s was even more emphatic than in Charles Darwin’s *On the Origin of Species*, especially the later editions where Darwin flirted with Lamarck.³⁵ As Gould pointed out,³⁶ the ethos of the times was unambiguously pan-adaptationist, and as he showed, textbooks following the 1959 Darwin centennial celebrations extolled “the sufficiency of natural selection [cumulative selection] to craft the entire range of evolutionary phenomena at all scales, ecological to geological.”³⁷ In one text, the authors argued that an organism is a mere “bundle of interacting adaptations. Most all the features of all living things are adaptations.”³⁸ Another author claimed: “Natural selection... [is the] finger beckoning to the otherwise unguided heredity of an animal type. All other principles and facts of evolution may be satisfactorily related to it or explained by it, and the century following 1859 has seen Darwin triumphant.”³⁹

However, the neo-Darwinian consensus was not without its detractors, and by 1985 there were some “flies in the ointment.” In addition to the celebrated and very widely read Gould and Lewontin “spandrel paper” criticizing the “pan-adaptationist” stance of the synthesis,⁴⁰ there was Gould’s later celebrated quip describing Darwinian explanations in many instances as no more than “just so stories.”⁴¹ (Jerry Fodor and Massimo Piattelli-Palmarini echo this sentiment in their recent book *What Darwin Got Wrong*.⁴²) At the same time, Gould, working with Niles Eldredge, formulated the punctuational model, which highlighted the lack of transitional forms in the fossil record, a fact captured by that other Gouldian quip that the absence of transitional forms was “the trade secret of paleontology.”⁴³ Gould, perhaps more than any other modern scholar, promoted the structuralist perspective in *Structure of Evolutionary Theory* by reviewing sympathetically the views of some of the leading nineteenth- and twentieth-century structuralists and criticizing the pan-adaptational stance.

Another straw in the wind was the controversy which erupted in the late 1970s and

early 1980s over the radical cladism (often referred to as pattern cladism) of Colin Patterson and other researchers at the Natural History Museum in South Kensington in London. (Cladism is a method of classifying organisms by their shared novel features alone without regard to any evolutionary assumptions.) New brochures and displays explaining the new cladistic approach to systematics implied that the fossil record contained no direct ancestral species, but only sister species, a claim that conveyed the implicit message for all to see that the main taxa are distinct and not led up to by transitional forms.⁴⁴ *Nature* thundered against the cladist brochures and displays in a hysterical editorial entitled “Darwin’s Death in South Kensington” and pointedly cited a brochure that contained what the editorial referred to as “weasel words,” namely, “if the theory of evolution is true.”⁴⁵

Given the sorts of claim made by some of the more radical cladists at the time, it is easy to understand *Nature*’s concern! For example, Keith Thompson commented on pattern cladism: “To the thesis of Darwinian evolution... has been added a new cladistics antithesis which says that the search for ancestors is a fool’s errand, that all we can do is determine sister group relationships of monophyletic taxa based on the analysis of derived characters.”⁴⁶ For a scholarly review of the controversies raised by the so-called pattern cladists in London and at the American Museum of Natural History in New York during the 1980s and 90s, see Chapter 6 in David Williams and Malte Ebach’s *Foundations of Systematics and Biogeography*.⁴⁷

There also was the troubling view of the Japanese geneticist Motoo Kimura,⁴⁸ who alluded to the growing evidence that much evolutionary change at the molecular level was neutral and had in many instances continued at a uniform rate. Kimura’s view was heresy at the time, when the conventional view was that the great majority of the bases in the genome were functional. His suggestion was seen to pose a major challenge to the pan-selectionism of the Synthesis and led to the so-called neutral theory of evolution.

Despite these other expressions of dissent, *Evolution: A Theory in Crisis* represented one of the very few publications in the 1980s to argue for the heretical possibility that nature might be fundamentally a *discontinuum* of isolated and unique Types unlinked by functional intermediates of the sort demanded by Darwinism. Few other publications attempted such a systematic critique of the whole Darwinian framework, and specifically of its core claim that cumulative selection is the sole or major engine of organic change and that all the order of nature and all evolutionary novelty can be accounted for by a simple extrapolation of microevolution to macroevolution.⁴⁹

Things are much changed today!

1.3 The Growing Critique

Since *Evolution: A Theory in Crisis* was published, there have been massive advances and discoveries in many areas of biology, including paleontology, genomics, and developmental biology. In 1985 the genome project was just launched, and researchers in developmental biology were just beginning to apply the new genetic knowledge to provide a detailed molecular genetic description of development. The new field of “evo-devo” (evolutionary developmental biology) was just emerging, as were the first hints of a new epigenetic paradigm,⁵⁰ with the realization of the importance of self-organizational

phenomena as a generator of emergent order beyond the genes, i.e., non-Darwinian “order for free.”⁵¹

During the subsequent three decades, these developments have transformed biology, and particularly evolutionary thought, leading to a growing and sustained critique of Darwinian pan-selectionism in many quarters that echoes some of the main themes of my earlier book. Indeed, it is widely acknowledged that one of the major challenges confronting evolutionary biology today is explaining the origin of the novel homologs that define and at the same time isolate the taxa. The recognition that there are indeed taxa-defining novelties is an implicit acknowledgement that the gaps may be real, part of the natural order, and not sampling errors—the core axiom upon which the nineteenth-century doctrine of the Types was based.

In *Homology, Genes, and Evolutionary Innovation* (2014), Günter Wagner, a leading researcher in the field of evo-devo, makes his sympathies with pre-Darwinian notions of the Type obvious. Questioning the notion that the homologs are “nominal kinds... simple arbitrary summaries of phenotypic structure and variation,” Wagner asks whether they are instead “natural kinds,” a possibility which he describes as “highly controversial.”⁵² Controversial or not, the very use of the term “natural kinds” by a leading mainstream researcher interested in evolutionary causation is illustrative of just how far skepticism of classic Darwinism has gone in some quarters.

Richard Prum and Alan Brush, the researchers who elucidated the development of the feather, speak for many workers in the evo-devo field when they write:

Recently, Wagner and colleagues... proposed that research on the origin of evolutionary novelties should be distinct from research on standard microevolutionary change, and should be restructured to ask fundamentally different questions that focus directly on the mechanisms of the origin of qualitative innovations. This view underscores why the traditional neo-Darwinian approaches to the origin of feathers, as exemplified by Bock (1965) and Feduccia (1985, 1993, 1999), have failed. *By emphasizing the reconstruction of a series of functionally and microevolutionarily plausible intermediate transitional states, neo-Darwinian approaches to the origin of feathers have failed to appropriately recognize the novel features of feather development and morphology, and have thus failed to adequately explain their origins.* This failure reveals an inherent weakness of neo-Darwinian attempts to synthesize micro and macroevolution. In contrast, the developmental theory of the origin of feathers focuses directly on the explanation of the actual developmental novelties involved in the origin and diversification of feathers (Prum 1999). Restructuring the inquiry to focus directly on the explanation of the origin of the evolutionary novelties of feathers yields a conceptually more appropriate and productive approach.⁵³

In the same vein, Douglas Erwin entitled one of his papers “Macro-evolution Is More than Repeated Rounds of Microevolution”;⁵⁴ and in another paper, Erwin and colleague Eric Davidson argued that micro-evolutionary changes are not able to account for the origins of or enact radical changes to what they termed core gene regulatory networks that are involved in generating the basic morphological motifs in all organisms.⁵⁵ Jerry Coyne,

a committed Darwinist, restates explicitly Erwin and Davidson's rejection of the extrapolation from micro- to macroevolution in his review of their paper:

Davidson and Erwin [propose] that the origin of higher level clades, such as phyla, involves mechanisms other than the normal micro-evolutionary processes thought to cause speciation. They claim that "classic evolutionary theory, based on selection of small incremental changes" cannot provide "an explanation of evolution in terms of mechanistic changes in the genetic regulatory program for development of the body plan."⁵⁶

Günter Wagner, mentioned earlier, is equally skeptical of the micro-evolution to macroevolution extrapolation and claims that the origin of major novelties may be inexplicable via gradualistic, bit-by-bit, Darwinian steps. One of his main points in *Homology, Genes, and Evolutionary Innovation* is that while microevolutionary changes may throw light on the origin of small-scale novelties, they may do nothing to explain macroevolutionary novelties such as the major higher-taxa-defining novelties discussed in this book. Wagner writes:

The question of how complex body plans arise is *not within the reach* of population genetics [defined as the change in gene frequencies in populations, i.e., microevolution] neither are the questions on how complex organisms can arise from random mutation and selection.⁵⁷

Another key point in Wagner's book is the claim (echoing Owen's distinction between homologs or "primal patterns" and their adaptive masks) that the processes which lead to major evolutionary novelties are different from those that cause adaptive modifications. Wagner argues:

Novelties likely require large scale reorganizations of the gene regulatory network. Gene regulatory network reorganization involves... the creation of novel cis-regulatory elements. In contrast adaptive modifications often involve only the modification of existing cis-regulatory elements.⁵⁸

An additional dissenting voice is Scott Gilbert, who confessed recently: "I'm on record in a 1996 paper saying that if the population genetics model of evolutionary biology isn't revised by developmental genetics, it will be as relevant to biology as Newtonian physics is to current physics."⁵⁹

Many recent publications touch on aspects of the current ferment, including Pigliucci and Müller's *Evolution, the Extended Synthesis*,⁶⁰ Wallace Arthur's *Evolution: A Developmental Approach*,⁶¹ Suzan Mazur's *The Altenberg 16*, and Fodor and Piattelli-Palmarini's *What Darwin Got Wrong*.⁶² Part One of the last-named book provides a highly critical review of the present status of classic Darwinism. The authors cite many current researchers in evo-devo to establish that there is widespread dissatisfaction with the micro- to macro- extrapolation, and argue that natural selection "can't be the *whole* story about how phenotypes evolve."⁶³ They go on to say: "In fact, as we read the current literature... *that isn't seriously in dispute these days*."⁶⁴ Basing their skepticism on the "evo-devo constraints paradigm" that informs so much research in evolutionary biology today, they write:

Contrary to traditional opinion, it needs to be emphasized that natural selection

among traits generated at random cannot by itself be the basic principle of evolution. Rather there must be strong, often decisive, endogenous constraints... on the phenotypic options that exogenous selection operates on.⁶⁵

Fodor and Piattelli-Palmarini conclude in words which echo the position I will defend throughout this work (also echoing Owen's distinction between homolog [the melody] and adaptive mask [tuning the piano]): "We think of natural selection as tuning the piano, *not as composing the melodies*. That's our story, and we think it's the story that modern biology tells when it's properly construed."⁶⁶

Admittedly, there are still many prominent figures such as Michael Ruse,⁶⁷ Jerry Coyne,⁶⁸ Daniel Dennett,⁶⁹ and Richard Dawkins⁷⁰ who strictly adhere to a pan-adaptational framework and to the notion that all macroevolutionary phenomena, from the origin of life to the origin of man, can be generally accounted for by the same mechanism, *cumulative selection*, that works at the microevolutionary level. But despite these dyed-in-the-wool Darwinists, *there is now a growing chorus of dissent within mainstream evolutionary biology!* A significant number of researchers, particularly in the new field of evo-devo, now argue that macroevolution requires an explanatory framework different from that of microevolution—thus confirming the underlying *leitmotif* of *Evolution: A Theory in Crisis*.

1.4 Preview

In this new book, I will argue that nature is still the fundamentally discontinuous system that I described in *Evolution*, consisting of a limited set of distinct stable material forms—the Types. And I will show, by a detailed consideration of several well-studied Type-defining homologs (including the tetrapod limb, the feather, and several others), that attempting to account for many of these homologs in terms of Darwinian cumulative selection poses intractable problems. I will show further that advances since 1985 are not supportive of Darwinian claims. On the contrary, the gaps or discontinuities alluded to in *Evolution* are "as wide as ever," especially when re-assessed from a structuralist perspective.

Moving beyond my original thesis in *Evolution*, and in keeping with structuralist notions, I will argue that many of the homologs appear to have never served particular functional ends. As I will make clear, this fact poses an additional challenge to Darwinian pan-adaptationism that greatly strengthens my overall critique of Darwinian functionalism.

I will also look at some Type-defining novelties that were not discussed in *Evolution*, including the enucleation of the mammalian red blood cell (a defining feature of class Mammalia), which was the focus of my own PhD thesis at King's College, London in the early 1970s.

As this book is already too long, I have deliberately omitted discussion of a swath of diverse challenges to Darwinian orthodoxy: those arising from the cost of selection (although this topic is touched on in the discussion of language evolution);⁷¹ those arising from rates of evolutionary change at the genomic level and increasing evidence that selection has only played a peripheral role in the assembly of genomes;⁷² and challenges arising from the implications of the ENCODE project, which suggests that much of the

genome may not be junk, as has been assumed for decades.⁷³

I also have omitted discussion of the problem of the equidistance or equal isolation at the molecular and genetic level of the members of specific clades from particular outgroup species. While this fascinating phenomenon is still as challenging as ever to the Darwinian narrative, it has been reviewed in detail by Shi Huang in a number of recent papers. He has shown that the equidistance phenomenon can only be accounted for if the origin of the different Types involved causal factors in addition to cumulative selection and drift and if the origin of the major types was saltational rather than the gradual process described by defenders of Darwinian orthodoxy.⁷⁴

Additionally, I have omitted any discussion of what seems to me an intractable problem in terms of the Darwinian framework: the origin of sentience and mind. Thomas Nagel recently highlighted this problem in his book, *Mind and Cosmos*.⁷⁵ Also omitted is any detailed discussion of the problem posed to Darwinism by the extreme adaptive complexity of living things. I still believe as strongly as when I wrote *Evolution* that random trial and error could never have actualized the sorts of complex adaptations that permeate the entire living kingdom from the molecular to the organismic levels. But many authors in the intelligent design (ID) movement have ably presented this argument over the past decade.⁷⁶

Although this book is primarily a critique of Darwinian incremental functionalism, as was *Evolution*, it is also—much more than my original book—a systematic defense of typology. Obviously, if the Darwinian enterprise fails and the taxa-defining homologs cannot be approached via adaptive continuums, then the idea that the Types are real categories in the world-order, no less than atoms or crystals, is supported by default.

I believe, along with Owen and many other nineteenth-century biologists, that life is an integral and lawful part of nature and that the basic forms of life are in some sense built into nature. I see this notion massively reinforced by the evidence of twentieth-century cosmology that the laws of nature are uniquely fine-tuned for life. Inevitably, therefore, this book is a defense of the typological world-view similar to that subscribed to by many nineteenth-century biologists: that the taxa-defining homologs represent a special set of natural forms which constitute the immutable building blocks of the biological world.

If the Types (or, more specifically, the homologs which define them) are indeed natural forms, their origin can never be explained by cumulative selection. Thus, Darwinism is bound to fail as a comprehensive explanation of life. In my concluding chapters, I will consider some new lines of evidence that support pre-Darwinian conceptions of taxa-defining “primal patterns” as emergent natural forms which arise from the self-organization of particular categories of matter, and the Types they define as ontologically real existents, part of the lawful and changeless order of the world.

At the outset, I would like to make an important point in defense of Owen and nineteenth-century “laws of form” biology as well as of the naturalistic thrust of this book. The idea that Darwin was the scientist and Owen was the mystic, that Darwinism is scientific while the opposing typological structuralist paradigm is quasi-mystical and unscientific, is simple nonsense. The truth is the reverse.

In preparing the final draft of this book, I came across a revealing quotation that

illustrates the profound bias in modern biological thought against Owen and nineteenth-century typology. In a paper published in 2009, leading evolutionary biologist Massimo Pigliucci claimed that starting with Darwin evolutionary biology “moved from natural theology to empirical science... Rather suddenly, the concept of evolution moved firmly away from being a quasi-mystical notion, and biology left Paley’s (1802) natural theology forever behind to enter the realm of respectable science, *just like physics had done two centuries before*.”⁷⁷

But how can a framework like Owen’s, which posits natural law as the explanation for the Types and the evolution of life, be unscientific?⁷⁸ And how can the Darwinian story, which is an historical narrative describing a series of contingent events, be “just like physics”?

Surely it is Owen’s views that are “just like physics,” while Darwin’s views are as far from physics as can be imagined! Of course, Owen was a Christian, a theist, and a teleologist.⁷⁹ Nevertheless, in seeking the natural laws that generate the basic organic forms characterizing life on earth, he was bringing the problem of the cause of organic form into the realm of experimental science.

In the next chapter, we will explore part of the reason why Darwin’s theory took hold as science—namely, the evidence of the power of natural selection. But as we shall see, that evidence is sharply limited in what it can explain about genuine novelties in living things.

2. Galápagos

Most of the organic productions are aboriginal creations, found nowhere else; there is even a difference between the inhabitants of the different islands... Considering the small size of the islands, we feel the more astonished at the number of their aboriginal beings, and at their confined range.

Charles Darwin, *Voyage of the Beagle* (1845), Chapter 17.

Six hundred miles off the west coast of South America, sitting almost exactly on the equator, lies a small archipelago consisting of eighteen barren volcanic islands scattered over a circle of sea some 150 miles across. The largest is about the size of Rhode Island, and four others are about one-quarter this size. Most are far smaller, and some are mere rocky outcrops in the vastness of the Pacific Ocean. Volcanic craters reaching up to three and four thousand feet surmount many of the larger islands. In places their flanks are studded with innumerable small volcanic cones and covered with large areas of barren volcanic scree.

The climate is remarkably cool for islands sited on the equator, the result of the Humboldt Current, which for many months of the year brings cold Antarctic waters northward along the western edge of South America. The Humboldt also brings rich nutrients to the surrounding seas, which teem with marine life. As a result of the cool waters, little rain falls on the coastal strips, which are arid and barren or vegetated by stunted shrubs. Well-vegetated areas and trees are mainly restricted to the central higher regions of the islands, which are often bathed in damp clouds. The islands are fringed in places by steep cliffs, in other places by flat rocky lava flows. Occasional sandy bays provide access from the sea. Remote, arid, and somewhat uninviting, the Galápagos Islands are a curiously inauspicious site for the first dawning of an intellectual revolution.

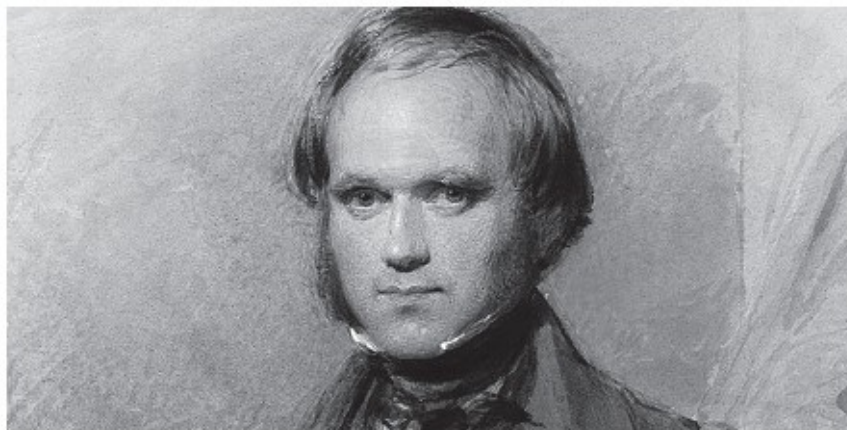


Figure 2-1. Charles Darwin. Drawn after he returned from the voyage of the *Beagle* in the late 1830s.

Named Galápagos from the Spanish word for saddle (galápagos), after the shells of the famous saddle-backed Galápagos tortoises, this remote archipelago entered the iconography of evolutionary biology because of the fateful visit in September 1835 of a British survey ship, the HMS *Beagle*. What Darwin saw on the Galápagos archipelago during his five-week stay in 1835 would be seminal in the development of his radical new evolutionary worldview. As Jonathan Weiner wrote in his wonderful book, *The Beak of*

the Finch: “These islands meant more to him than any other stop in his five-year voyage around the world. ‘Origin of all my views, he called them once.’”¹ The evolutionary significance for Darwin of the Galápagos and other similar oceanic biotas is highlighted by the fact that in the first edition of the *Origin*, Darwin devoted eighteen pages of discussion to the topic, a point alluded to by Gould.²

2.1 Microevolution

Among the most remarkable of all the unique species of the archipelago are a set of thirteen closely-related types of finch. Their close relationship is indicated by the fact that they all exhibit the same nest architecture, egg coloration, and complex courtship display³ and has been confirmed by recent DNA analysis.⁴ However, they are in many other respects distinct in terms of plumage, behavior (including feeding habits), and beak morphology. Each species is peculiarly adapted to a particular ecological niche on one or several of the islands of the archipelago and possessed of a unique beak morphology adapted to a particular type of food—seeds, insects, etc. In fact they are, as Weiner remarks, “spectacularly and peculiarly diverse.”⁵ In any suburban garden, they would all be judged as different species.⁶

Reflecting on this remarkable group of birds Darwin famously (and rightly) inferred: “Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends.”²

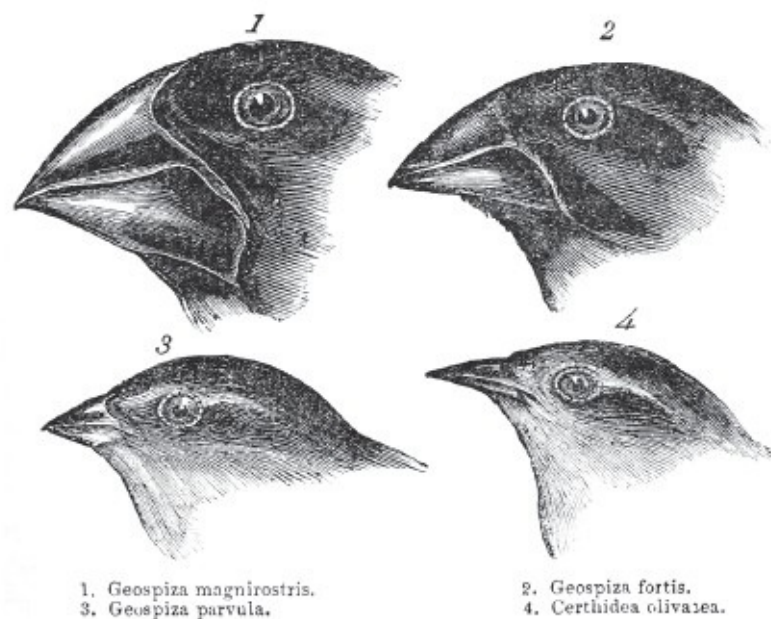


Figure 2-2. Galápagos Finches.

In other words, species were not specially created. Existing species had descended with modification from pre-existing species. This realization was for Darwin, as he later described it, “like confessing to murder,”⁸ so entrenched was the then universally accepted doctrine of the fixity of species. Darwin also inferred (again rightly, as the work of subsequent researchers on Galápagos has amply confirmed⁹) that the major causal mechanism responsible for their adaptive divergence—the shaping of their beaks for example—is the simple mechanism of natural selection. More specifically, the cumulative selection of successive small adaptive changes has fashioned each species step-by-step

with a morphology perfectly suited to thriving in “its” special ecological niche.¹⁰

Moreover, Darwin also speculated (in Chapter 4 of the *Origin*) as to how cumulative selection might gradually lead to increasing morphological and behavioral specialization of well-adapted varieties, which over time might lead to the origin of new species.¹¹ Although there is still some question as to whether the species of finches are “true species” and not just well-differentiated subspecies,¹² subsequent work on the finches has largely confirmed his basic intuition as is obvious from Weiner’s description of the extraordinarily painstaking research of Peter and Rosemary Grant over the past several decades.

Intriguingly as far as the beak forms are concerned, recent developmental genetic studies have thrown light on how the adaptive diversity might have been come about by revealing that the two genes involved in the generation of the different beak forms of the finches are used in all avian species to modulate beak form.¹³ One gene, *Bmp4*, encodes bone morphogenetic protein 4, and the other gene encodes calmodulin (CaM), a molecule involved in mediating Ca²⁺ signaling. If the *Bmp4* gene is turned on early and at high levels in the beak of a developing bird, the beak becomes deeper and broader. When calmodulin is expressed at high levels in the beak of a developing bird, the beak becomes elongated. These genes are fairly similar to one another in different finch species, but they are turned on and off at different times. Altogether the evidence suggests that, over evolutionary time, simple genetic changes in the patterns of expression of these genes (e.g., when and where they are turned on and off) produced the diverse set of finch beak shapes we see today. These studies have shown that the diversity of beak morphology can be readily explained by the gradual, functional fine-tuning of microevolutionary changes in a few key genes that shape the form of the beak in all birds. Just as it is easy to envisage gradual morphological change in beak form to serve functional purposes, so it is relatively easy to envisage the fine-tuning of the expression of these two key morphogenetic genes to actualize these changes.

As far as the evolution of finch beaks is concerned, there is no need either at the morphological or genetic level to call for any causal agency other than cumulative selection. Here I concur with classic Darwinism. The beaks are clearly adaptations and their evolution is entirely explicable within a classic functionalist framework. As the different beak forms are clearly contingent adaptations which evolved to meet the unique environmental demands on a group of volcanic islands that only emerged from the Pacific a few million years ago, their evolution is beyond any structuralist or “laws of form” type of account.

As Darwin explains in the introduction to the *Origin*, it was because he had in natural selection a mechanism that might explain “how the innumerable species inhabiting this world have been modified so as to acquire that perfection of structure and coadaptation which most justly excites our admiration” that he finally set about composing his great work.

The lesson of the Galápagos, and one of the repeated mantras of *Evolution: A Theory in Crisis* (see Chapters 2 and 4) is simply this: Cumulative selection will work its magic as long as the novelty of interest is adaptive and there is a functional continuum (at the morphological or genetic level) leading from a putative ancestor species or structure A to

a descendant species or structure B. Even in the absence of any empirically known functional continuum, if a convincing hypothetical continuum can be readily envisaged linking A to B, then the possibility of B “evolving from A” via cumulative selection can be plausibly inferred.¹⁴

To repeat: Where an evolutionary novelty can be construed as being adaptive and where a sequence of small incremental changes leading to the novelty can be cited (or envisaged), *functionalist accounts are clearly plausible*. This is the case with the Galápagos finch beaks and many other cases of microevolution, but as this book shows in the chapters ahead, adaptive sequences, either empirically known or hypothetical, *are* lacking in the vast majority of cases of macroevolution, especially those involving the evolutionary actualization of the taxa-defining homologs—e.g., leading from the fin of a fish to the tetrapod limb, from the scale of a reptile to the feather of a bird, or from a “pine cone” or some other putative antecedent structure to the angiosperm flower.

2.2 Cumulative Selection as Causal Agency

That cumulative selection necessitates a long series of adaptive intermediates linking ancestor with descendant was conceded by Darwin in many places in the *Origin*. Indeed, over and over again he confesses the need for “innumerable transitional forms.”¹⁵ Acknowledging “that natural selection generally acts with extreme slowness,”¹⁶ he admits that “as natural selection acts solely by accumulating slight, successive favorable variations, it can produce no great or sudden modifications; it can only act by short and slow steps.”¹⁷ And he declares, famously: “If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous successive slight modifications, my theory would absolutely break down.”¹⁸

Darwin, perhaps more than any subsequent evolutionist, was committed to an extremely gradualistic model, insistent that evolution by natural selection can never take jumps,¹⁹ and that the individual variants upon which selection acts are very small. Indeed, in the *Origin* he talks about the differences that natural selection exploits being “absolutely inappreciable by an uneducated eye—differences which I for one have vainly attempted to appreciate.”²⁰ Holding the individual steps to be so extremely small, it is no wonder Darwin envisaged the building of organic complexity to have required “an interminable number of intermediate forms,”²¹ and he even concedes that a reader who does not admit “how vast have been the past periods of time, may at once close this volume.”²²

Self-evidently, to go from ancestor A to descendant B via cumulative selection does require, as Darwin rightly infers, a long sequence of adaptive transitional forms. But there is another compelling reason for postulating “an interminable series of intermediates,” if selection is to be the causal engine directing the actual evolutionary change. Although Darwin never explicitly expands on the point, Gould brings it out with great clarity in his *The Structure of Evolutionary Theory*, where he shows that natural selection can only play a creative role in molding new evolutionary forms if two stringent conditions are met:

- (1) if nothing about the provision of the raw materials—that is, the sources of variation—imparts direction to evolutionary change; and (2) *if change occurs by a long and insensible series of intermediary steps, each superintended by*

*natural selection—so that “creativity” or “direction” can arise by the summation of the increments.*²³

Regarding the sources of variation (condition 1), Gould reminds us that:

Variation must exist in sufficient amounts, for natural selection can make nothing, and must rely upon the bounty thus provided [by natural variation]; but variation must not be too florid or showy either, lest it become the creative agency of change all by itself. Variation, in short, must be copious, small in extent, and undirected...

If the variations that yielded evolutionary change were large—producing new major features, or even new taxa in a single step—then natural selection... as a theory of evolutionary change, would perish... variation itself would emerge as the primary, and truly creative, force... For this reason... saltationist (or macromutational) theories have always been viewed as anti-Darwinian.²⁴

Commenting on the necessity that evolutionary change occurs via a long series of incremental steps (condition 2), he continues:

We now come to the heart of what natural selection requires... in going from A to a substantially different B, evolution must pass through a long and insensible sequence of intermediary steps—in other words... ancestor and descendant must be linked by a series of changes, each within the range of what natural selection might construct from ordinary variability. Without gradualism in this form, large variations of discontinuous morphological import—rather than natural selection—might provide the creative force of evolutionary change.²⁵

If these two conditions hold, as all Darwinian advocates assume that they do, then natural selection can be conceived of as Darwin did in the *Origin*: as the sole director and creative agent in evolution,²⁶ responsible for all the complexity and variety of life and the phylogenetic branching pattern of the tree of life. As I pointed out previously:

Darwin’s central and entirely unique claim in the *Origin* was not that natural selection occurs and is bound to eliminate the unfit... Rather, his revolutionary claim was that natural selection could be the main *creative agent* in evolution if it superintended the ever so gradual accumulation of tiny undirected mutations... Selection per se is not the defining characteristic of Darwinism, but only where it acts as the creative agent, building complexity incrementally resulting in what Gould terms “additive aggregates.”²⁷

Consequently, Darwin’s interminable series of transitional forms is necessary for straightforward mechanistic reasons (how else can one get from A to B by cumulative selection?), but it is also essential if the sole agency of change is to be natural selection. Where a complex adaptation—no matter how complex—can be reached in a series of tiny adaptive steps, then natural selection can indeed function, in Dawkins’s description,²⁸ as a *blind watchmaker* and change A into B no matter how complex the transition, without any other causal agency being involved. And it is this elimination of the need for any alternative or additional directive mechanism guiding the evolutionary process which is, for atheists and materialists like Dawkins and Dennett, its great attraction.

Here we touch on an important point, which needs emphasis: Organisms are complex systems, and their assembly during the course of evolution, by universal assent (e.g., Darwin, Fisher, Dawkins, Fred Hoyle, Dennett), could never have occurred by “pure chance.” Some form of direction is essential! This is why, as stressed below (see Chapter [11](#)), both Darwinists and their opponents reject the idea that undirected chance (or trial and error) could assemble any sort of complex biological structure. Only if evolution is directed by some mechanism can the complexity of living things be explained.

Darwin’s theory of cumulative selection was—and is—a brilliantly simple theory to provide an account for *adaptive* design and *adaptive* order in the living world without recourse to additional guidance from any other agency. Daniel Dennett calls it the “best idea anyone has ever had.”²⁹ Yet clever though it may be, it can only work, firstly, if the “form” of interest can be shown to be adaptive and, secondly, if the “form” is led up to via a functional continuum through which cumulative selection can find its way and work its magic. And this, to a very large extent, is why so many in the mainstream academic community, enamored as they are with the Darwinian worldview, must look the other way, if—as it is certainly the case, as I will show—many of the taxa-defining homologs actualized during the course of evolution have *never* been shown to be adaptive and even in the case of those homologs which are apparently adaptive, functional continuums are either unknown or very hard to envisage. To acknowledge their absence is to acknowledge that the paths of evolution must have been ordered and directed by additional causal factors, i.e., that cumulative selection is not the sole or even the major directive agency.

2.3 Eliminating Telos and Teleology

Because cumulative selection acts only to adapt an organism to its immediate environmental conditions, without any concern for what the long-term consequences of any specific adaptation might be or where it might lead, it has no foresight.³⁰ And without foresight, the ends or designs it can achieve are those (to employ Dawkins’s aptly-chosen analogy) of a “blind watchmaker.”³¹ It is the absolute blindness of the process that is its hallmark and carries such radical implications.³² As Ernst Mayr put it, “The truly outstanding achievement of the principle of natural selection is that it makes unnecessary the invocation of ‘final causes’—that is, any teleological forces leading to a particular end. In fact, nothing is predetermined. Furthermore, the objective of selection even may change from one generation to the next, as environmental circumstances vary.”³³

By providing a mechanism to account for order and adaptive design without a designer, natural selection upended the biological argument to design that had been the mainstay of English natural theology since the seventeenth century. It also upended the widespread belief of many of the structuralists and typologists before Darwin (including Richard Owen and many other leading nineteenth-century biologists)³⁴ that the paths of evolution were predetermined by natural law; and it overturned the notion of a lawful biology where the major Types were as much a part of the world order as were inorganic forms. After Darwin, all such causal theories came to be seen as “skyhooks,” as Dennett contemptuously refers to them.³⁵

It is worth noting that the typologists of the nineteenth century, though seeing life’s forms as the result of laws and hence “natural,” also interpreted these laws as causal agents within a comprehensive teleological framework. Louis Agassiz, for example, saw

the Types as ideas in the mind of God³⁶ and saw the whole taxonomic system as part of God's grand plan of creation. In his *Essay on Classification* he argued: "To me it appears indisputable, that this order... [is] in truth but translations into human language of the thoughts of the Creator."³⁷ Owen also viewed nature's order as the result of a Divine plan. He even went so far in his *On the Anatomy of Vertebrates* to declare "the Horse to have been pre-destined and prepared for man."³⁸ However, although Owen saw nature as the result of design, he believed that God had used natural laws to achieve His ends.³⁹ As Owen commented, one of his aims was "to show in these structures [i.e., "the parts and organs" of vertebrate animals] the evidence of a predetermining Will, producing them in reference to a final purpose."⁴⁰

2.4 From Microevolution to Macroevolution

If Darwin had gone no further than providing an explanation for the evolution of finch beaks and other cases of microevolution, he might have gone down as a notable Victorian naturalist. But Darwin (as I pointed out in Chapters 2 and 3 of *Evolution: A Theory in Crisis*) went much further. He became one of the most influential thinkers in Western intellectual history by making the radical claim that the origin of all the novelties in the history of life, all the taxa-defining traits, all complexity, all order, could be explained by extending or extrapolating, over great periods of time, the same simple, undirected, and 100-percent-blind mechanism of cumulative selection that fashioned the different finch beaks on Galápagos.

The significance of Darwin's extrapolation can hardly be exaggerated. If it was correct, the problem of evolution would be essentially solved, and the emergence of all species, including mankind, finally explained without any recourse to teleology or "laws of form." And for some current hardline Darwinists, the problem of evolution is indeed regarded as solved: New forms of life are the outcome of the machinations of a "blind watchmaker." Daniel Dennett writes: "The fundamental core of contemporary Darwinism... is now beyond dispute among scientists... the hope that it will be 'refuted' by some shattering breakthrough is about as reasonable as the hope that we will return to a geocentric vision and discard Copernicus."⁴¹ Similarly, according to Richard Dawkins, "Darwinism is true, not just on this planet but all over the universe wherever there is life to be found."⁴²

The extrapolation from micro- to macroevolution is certainly seductive. But as I pointed out in *Evolution* (Chapter 4) the fact that an unseeing watchmaker can work his magic on a small scale (as on the Galápagos), the fact that Darwin's mechanism works in a restricted area, the fact that adaptation exists in nature—none of this warrants the assumption that *all* the order of nature (including *all* the Type-defining novelties) is adaptive and can be assembled via functional continuums. There is an almost universal precedent, as the history of science testifies, that over and over again theories that were once thought to be generally valid have proved eventually to be only valid in a restricted sphere.⁴³

Moreover, the greatly-touted success of Darwinism in the restricted field of *microevolutionary* adaptation—classically illustrated by its ability to account for the adaptive diversification of the fauna of Galápagos and other oceanic islands⁴⁴—is a two-edged sword. While these cases demonstrate that cumulative selection can generate small

degrees of adaptive evolutionary change in tiny incremental steps, they illustrate that the mechanism depends on the satisfaction of a demanding condition: *Descendant species (or structures such as novel homologs) must be linked with their putative ancestral species (or structures) via a long series of empirically known or theoretically envisaged functional sequences of intermediate forms.*

This need for adaptive continuums brings us to the nub of the problem, the core contention of *Evolution: A Theory in Crisis*, and the major point defended here: Practically all the novel, taxa-defining homologs of all the main taxa are *not* led up to via adaptive continuums. Moreover, as argued later in this book, many of these novel *Bauplans* do not convey any obvious impression of being adaptive—a fact admitted by Darwin in the *Origin* with regard to one of the classic *Bauplans*, the pentadactyl design underlying the tetrapod limb. It is ironic that the very evidence for believing that microevolution has indeed occurred in cases like the finches—an empirically known or readily envisaged continuum of forms leading from an ancestral form A to descendant form B—is precisely the evidence that is lacking when attempting to account for macroevolution and the origin of the defining features (feathers, hands, mammary glands, hair, the placenta, flowers, body plan, etc.) of the major taxa.

As we will see in coming chapters, it is widely acknowledged—indeed common knowledge—that the great majority of novelties which define the taxa are not led up to via the adaptive continuums that might have endowed selection with causal directive agency. Unfortunately, very few are prepared to follow the logical implication of this absence: namely, that the origin of the basic Types of nature must have been determined or directed by causal factors other than gradual cumulative selection.

In the next chapter, we will begin to examine just how widespread taxa-defining novelties actually are—and how many evolutionary biologists are now acknowledging that evolutionary theory has yet to account for them.

3. The Hierarchy of Nature

... that great and universal feature in the affinities of all organic beings, namely, their subordination in group under group.

Charles Darwin, *On the Origin of Species* (1872), Chapter 14.

One of the major achievements of pre-Darwinian biology was the discovery that the living world is organized into a hierarchy of ever more inclusive classes or Types, each clearly defined by a unique homolog or suite of homologs possessed by all the members of the Type and which in many cases have remained invariant in divergent phylogenetic lines for tens or hundreds of millions of years.¹

Seeking an explanation for the distinctness of the Types and determining their ontological status was seen to be one of the major tasks of nineteenth-century biology. As mentioned in the Introduction, virtually all pre-Darwinian biologists, and many after Darwin, saw the Types as immanent and invariant parts of the world-order, no less than crystals or atoms.²

There is currently a widespread impression that pre-Darwinian biologists derived their discontinuous-typological conception of nature from all sorts of discredited metaphysical beliefs. This view has been severely criticized by recent researchers and shown to be largely a myth created by twentieth-century advocates of the neo-Darwinian evolutionary synthesis³—what Ron Amundson calls “Synthesis Historiography.”⁴ As Amundson shows, whatever their metaphysical leaning, pre-Darwinian biologists did not derive their view of the Types as changeless components of the world order from any *a priori* metaphysics (idealistic morphology, transcendental anatomy, essentialism, Platonism, etc.) but from solid empirical observations. Amundson comments: “We will fret over their metaphysics no more than we fret over Kepler’s... [T]hey do not deserve the disdain to which they have so long been subject.”⁵ As Amundson points out, from the time of Geoffroy and von Baer in the early nineteenth century, the belief that the homologs that define the morphological Types were real existents in the order of things persisted among scientists into the twentieth century:

Types were hypothesized in order to account for the wide and complex patterns of organic form... There is nothing foolish about them; some of the best thinkers of the nineteenth century were involved in their use. With a few exceptions (e.g., Agassiz), the metaphysical aspects of types were all but forgotten by the 1850s, whereas the explanatory aspects continued to be important throughout the century. It is impossible to understand the science of that period if we dismiss these theories as perniciously and metaphysically idealist.⁶

The nineteenth-century structuralist conception of the Type, and of an ascending hierarchy of taxa or Types of ever-widening comprehensiveness as immanent features of nature, was close to the classic Aristotelian worldview.⁷ But it was based on the *facts* of biology, not on a philosophical *a priori* assumption—Aristotelian, Platonic, or otherwise.

Today, 150 years after Darwin, Owen’s “biological atoms” are still as distinct as ever.

The vast majority of all organisms can be assigned to distinct and unique classes based on their possession of particular defining homologs or novelties which are *not* led up to via Darwin's "innumerable transitional forms." Moreover, providing an explanation for the origin and fundamental nature of the taxon-defining homologs, from the origin of the cell system (a *Bauplan* shared by all life on earth⁸) to the origin of human language (a homolog shared by all members of the human race) remains a major unfinished task.

The hierarchy of ever more inclusive Types defined by one or more novel homologs provides the basis for the natural system and is also reflected in the biology of each individual species. Man, for example, manifests in the design of his body the vertebrate *Bauplan* or primal pattern (shared by all vertebrates); in his arm and leg, the tetrapod homolog (shared by all terrestrial vertebrates); the amniotic membrane (shared by all higher vertebrates); and in his diaphragm, a defining mammalian homolog shared by all mammals. Each organism can be considered to be built up out a suite of basic homologs that constitute its anatomy.

Note also that the number of taxon-defining homologs is enormous. As Rupert Riedl comments: "Characters that have been shown to define a taxon are fixed within the entire set of its members... and given that about 100,000 taxa (from genera to phyla) have already been established and verified by systematicists, based on perhaps 10 characters for each... [this implies a very] large number of hierarchically fixed homologues."⁹

3.1 Type-defining Homologs

In this section I describe a few classic and well-known taxon-defining homologs.

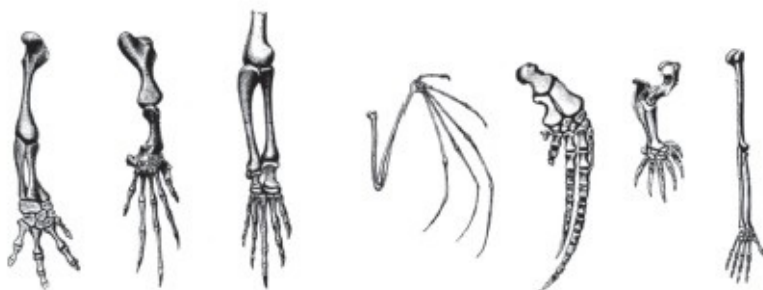


Figure 3-1. The Pentadactyl Limb. This shows the structure of the forelimbs of various vertebrate species. Left to right: salamander, toad, crocodile, bat, whale, mole, and human. The digits are displayed with digit one, the most anterior digit (e.g., the thumb in man) to the right. Although in some species the number of digits is reduced, no terrestrial vertebrate has more than five true digits. The salamander has four, having lost digit five. The mole has a pseudo digit derived (as in the case of the panda) from a modified carpal bone and positioned anterior (to the right in the figure) of digit one.

The Pentadactyl Limb

All extant terrestrial vertebrates (and their aquatic descendants, such as whales, seals, and turtles) are grouped within the clade Tetrapoda, and possess a unique defining *Bauplan* known as the pentadactyl limb, consisting of one proximal bone (the humerus in man), two more distal bones (the radius and ulna in man), and five digits as well as other unique features. This basic pattern has been conserved in all tetrapods for 400 million years. (See Figure [3-1](#).)

The Feather

All modern birds, and some related groups of reptiles,¹⁰ possess closed pennaceous contour feathers consisting of a central shaft or rachis. (See Figure 3-2.) Fused to the rachis are barbs, and attached to each barb are hooked distal barbules pointing towards the tip of the feather and inter-locking grooved proximal barbs pointing to the base of the feather. (See Figure 3-3.) All organisms possessed of this defining feature can be unambiguously assigned to a unique clade belonging to the more inclusive dinosaur clade Theropoda.¹¹



Figure 3-2. The Pennaceous Feather. (1) the vane; (2) rachis; (3) barb; (4) afterfeather; (5) hollow shaft or calamus.

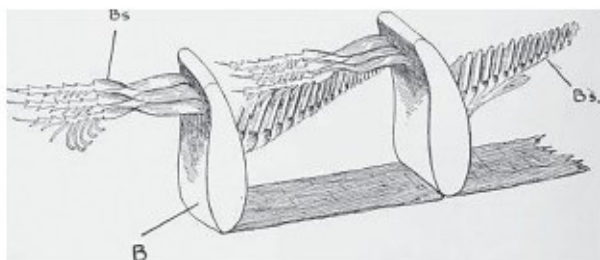


Figure 3-3. Feather Parts. The interlocking barbules (Bs) that hold the barbs (B) in the vein together (distal hooked barbules pointing to tip of feather and grooved proximal barbs pointing to base).

The Insect Body Plan

All living insects possess a set of unique defining features. The insect body has three divisions: head, thorax, and abdomen. The thorax consists of three segments, each bearing a pair of legs, making a total of six legs altogether. Eleven segments can be recognized in the abdomen of most juvenile insects, and although some insect adults—including coleoptera (beetles) and hymenoptera (wasps, bees, ants, etc.)—have fewer than eleven segments, no insect has more than eleven. The legs of all insects consist of no more than five components: the coxa, the trochanter, the femur, the tibia, and the tarsus. (See Figures 3-4 and 3-5.) The tarsus itself is typically divided into five subsegments. The insect mouth, in all the diverse species, consists of four parts from front to back: the labrum, the mandibles, the maxillae, and the labium. Finally, all insects possess two antennae, which are mobile jointed appendages. Invertebrates that possess these defining features can be unambiguously assigned to the class Insecta.

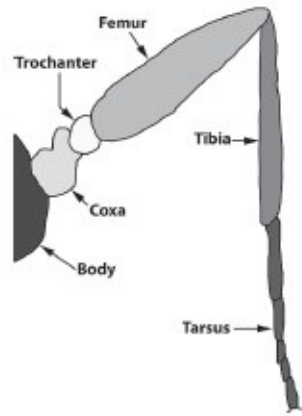


Figure 3-4. The basic parts of the insect limb.

Further, all wings in extant species of insect are based on the same underlying homologous taxon-defining venation pattern, and each order of insects has its own taxon-defining variation on this underlying theme. As Penelope Gullan and Peter Cranston point out in their well-known text, *The Insects*: “All winged insects share the same basic [venation pattern]... Wing venation patterns are consistent within groups (especially families and orders), but often differ between groups... [and are] major features used in insect classification and identification.”¹²

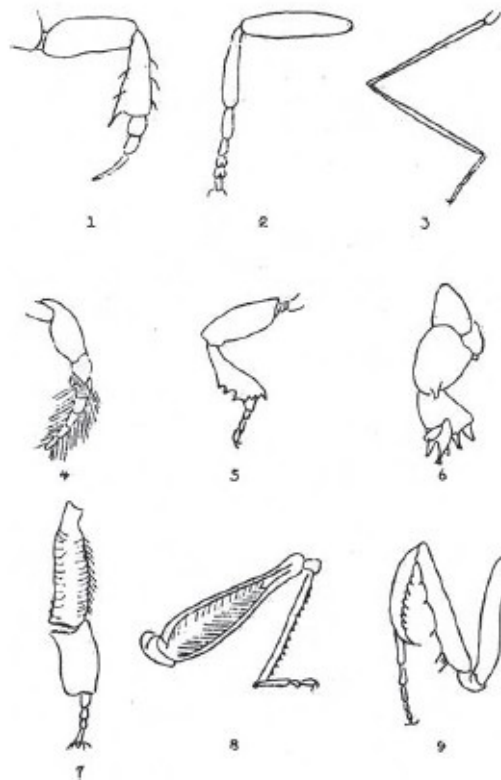


Figure 3-5. Insect Limbs. How the same parts are used in various limbs adapted to perform very different functions in different species: (1) biting louse (note sharp claw at the end of the Tarsus); (2) house fly (note the claws at the end of the tarsus for holding on to the substrate); (3) water strider (skates on the surface of the water on thin limbs which do not penetrate the surface); (4) water beetle (note fringe of hairs which create a paddle); (5) engraver beetle (note the jagged projections from the tibia which assist it in burrowing through wood); (6) mole cricket forelimb (note how limb ends in spade-like tibia and tarsus for digging through the soil); (7) honey bee hind limb, tibia, and tarsus (note the fringe of hairs surrounding the pollen basket on the tibia); (8) grasshopper hind limbs (note the enlarged femur which contains the powerful jumping muscles); (9) praying mantis forelimbs (note the sharp projections on the femur for grasping prey).

The Flower

One of the defining *Bauplans* of all higher angiosperms (eudicots) is the flower, consisting of a remarkable pattern of four nested concentric whorls: an outermost whorl of sepals, surrounding a whorl of petals, which in turn surrounds a ring of stamens and, in the center, a small circular region containing the pistil. Moreover, each taxon of angiosperms is defined by a novel floral formula, which is a variation on this basic theme (like the wing venation patterns in insect orders, which are all variations on the more inclusive generic ground plan), indicating the defining number and variation in sepal, petal, stamen, and carpel pattern characteristic of a particular taxon.¹³ Another defining novelty or homolog of the angiosperms is the set of unique cytological events which characterize the development of the female gametophyte (see description in Chapter 8) and double fertilization.¹⁴ Double fertilization occurs when the pollen tube reaches the embryo sac, after which one of the two haploid sperms released from the pollen tube fertilizes the egg cell, which develops into the embryo, while the other fuses with the two haploid nuclei of the central cell, which develops into the endosperm, which contains nutrients which feed the developing seedling.¹⁵ Different groups of angiosperms are also characterized by differences in the patterns of cell divisions that precede the formation of the female gametophyte. (See the further discussion of angiosperms in Chapter 8.)

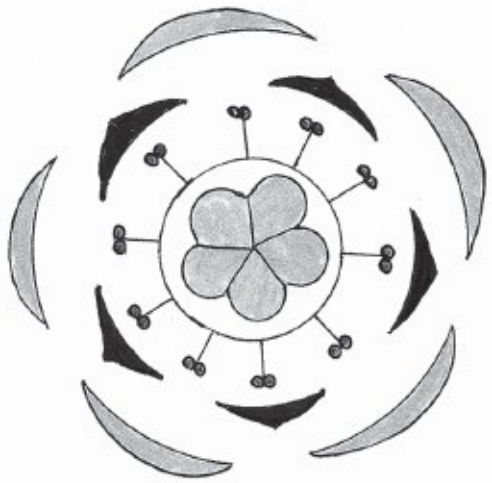


Figure 3-6. Flower. Showing series of concentric whorls from the outermost to the innermost: sepals, petals, stamens, and carpels.

The Amniotic Membrane

Another taxon-defining homolog with no antecedent structure in any ancestral form is the amniotic membrane which encloses a protective fluid-filled cavity surrounding the embryo possessed by all reptiles, birds and mammals, and which defines the clade Amniota.

Diagnostic Mammalian Traits

In the case of the class Mammalia, some of the suite of defining homologs which characterize the mammalian *Bauplan* are hair, an enucleated red cell, a diaphragm, mammary glands, and a laminar cerebral cortex consisting of six layers. These defining features are not possessed even in the most rudimentary form by any other vertebrate class. On the basis of this suite of characteristics, an organism may be definitively included in or excluded from the class Mammalia.¹⁶ In addition, virtually all mammals have only seven cervical vertebrae, including the giraffe [neck length nearly two meters],

mouse [length less than one centimeter], whale, elephant, and human. Only the sloths and manatees depart from this pattern.¹⁷ Also, nearly all extant placental mammalian orders, including our own, the Primates, have no more than forty-four teeth, and despite the many dental adaptations and loss of teeth, most placental mammals possess no more than four molars, three premolars, one canine and three incisors.¹⁸ The only significant departures from this pattern occur in Armadillos and extant Cetaceans.¹⁹

Centipedes

It not just the major taxa which are characterized by unique defining homologs or novelties. Centipedes, belonging to the clade Chilopoda, possess two remarkable taxon-defining novelties. First, the number of segments in centipede species varies from 27 to 191, but in every case the segment number is odd. No centipede with an even number of segments has ever been found.²⁰ Second, every centipede possesses a novel venom-injecting device, a poison claw, which is a drastically modified pair of limbs. As Wallace Arthur comments regarding this defining novelty: “No animals outside the Chilopoda possess a similar poison claw... So this... appears to have arisen only once in evolution and, at least as yet, has persisted in all the lineages that have descended from the original ‘ur-centipede.’”²¹ The centipede *Bauplan* including the poison claw and odd number of segments has remained unchanged for 420 million years.²²

Beetles

The beetles (Coleoptera)²³ have their own set of taxon-defining features. As described in *Imms’ General Textbook of Entomology* beetles are: “Minute to large insects whose fore wings, not used in flight, are modified into horny or leathery elytra which almost always meet to form a straight mid-dorsal suture: hind wings membranous, folded beneath the elytra, or often reduced or wanting. Mouthparts adapted for biting: ligula variably lobed. Prothorax large and mobile, mesothorax much reduced. Abdominal tergites often little sclerotized. Metamorphosis complete: larvae campodeiform [flattened body, well-developed feet] or cruciform, seldom apodous [without feet] with mandibulate mouthparts: pupae adecticous [no mandibles] and exarate [appendages moveable], rarely obtect [pupae encased in hard shell with appendages immobile].”²⁴ Antennae consisting of eleven segments and “genitalia retracted into abdomen.”²⁵ The *Bauplan* of the adult beetles has remained essentially unchanged for 300 million years.²⁶

Ants

Even less-inclusive taxa are often defined by very curious novelties that are not led up to via innumerable intermediate forms. For example, even the relatively low-level taxon of the ants (Family Formicidae), one of the families of the Hymenoptera, possesses the following defining characteristics: “Male and fertile female (queen) nearly always winged... workers wingless. 1st or 1st and 2nd abdominal segments of gaster scale-like or nodiform and well-separated from the part behind [the gaster]. Male gaster without an upturned terminal spine; worker with spur of fore tibia not much curved and not externally pectinate. Antennae elbowed and less clearly so in male.”²⁷ As well, all ants possess a unique novelty, a metapleural gland on the underside of their thorax.²⁸ These defining features of the ants were in place at least sixty-five million years ago when the major adaptive radiation of ants occurred at the end of the Cretaceous era and have remained

unchanged since then to the present day.²⁹

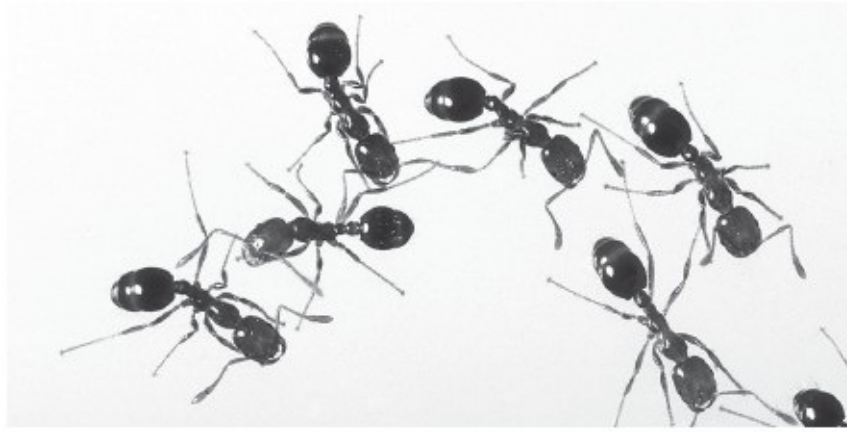


Figure 3-7. Ant. An image of ants showing elbowed antennae and first and second nodiform abdominal segments.

Butterflies

Another novel *Bauplan* that defines a low-level taxon is the ground plan of the largest group of butterflies, the Nymphalidae, consisting of several pattern elements, including eye spots and bands which are repeated in each subdivision of the wing that is bounded by veins.³⁰

Others

Finally, even individual species are often defined by unique novelties (autapomorphies in cladist terminology). Familiar examples are the unique shapes of the leaves of different species of plants and trees. In the case of man, language is an autapomorphy whose deep structure, as originally shown by Noam Chomsky, is the same in all extant human races and for which there exists no antecedent in any sub-human primate.³¹

3.2 The Reality of the Types

For readers subjected to popular and pervasive claims by evolutionary biologists that there are innumerable transitional forms of organisms,³² it might come as something of a surprise that there are unique taxon-defining novelties not led up to gradually from some antecedent form, and which remain invariant after their actualization for vast periods of time.

There is indeed something incongruous about the very notion of distinct taxa and genuine immutable “taxon-defining novelties”—more than 100,000 according to Rupert Riedl—in the context of the functionalist Darwinian framework, which implies that all taxa-defining traits should be led up to via long series of adaptive transitional forms! On such a Darwinian model, taxa-defining novelties should not exist; neither should distinct Types in which all members possess unique defining novelties not shared by the members of any other taxa. As I will try to clarify in Chapter 6, the apparent conflict between the widespread claim that there are many transitional forms³³ and the contrary claim that transitional forms are rare³⁴ or absent has arisen out of confusion of homologs with the Types they define.

Not surprisingly, there have been authors who have argued just this point: that the existence of taxon-defining characteristics is incompatible with the whole notion of gradual neo-Darwinian transformations. For example, Riedl has written: “If every

character were free to change in every direction, the living world would appear as a random chaotic mixture of patterns, and the single relationship left among their representatives would not relate to common ancestry but only to common functions, such as analogous limbs, horns, wings, jaws and so forth.”³⁵ The same point was explicitly made by John Beatty in a critique of radical cladism in the early 1980s. He argued that “pattern cladistics is not, after all, evolutionarily neutral. Rather, it is at odds with evolutionary theorising.” He went on to argue that systematists are justified in abandoning the search for defining characters because *if evolution occurs, taxa should have no “properties that are collectively necessary and sufficient for membership in the group.”*³⁶ On such a view there should indeed be *no* taxa-defining novelties.³⁷

Let me reiterate: If evolution has occurred as conceived of by Darwin, invariant taxa-defining novelties, not led up to via long sequences of transitional forms from some antecedent structure, *should not exist*. But exist they do! Riedl (a world authority on marine invertebrates and one of the foremost biological theorists in the last quarter of the twentieth century) was someone who definitely knew these facts, and he was moved to comment:

Although such fixation [the invariance of the taxa-defining traits] may not be self-evident to some of my colleagues, I must emphasize that in accepting the evolutionary history of taxonomic groups the fixation of homologues is a logical necessity. Thus for example, the chorda remains a chorda in all chordates from ascidians to man; the backbone remains a backbone in all vertebrates, from frog to python; and a particular digit remains the same digit in all tetrapods from horses to bats.³⁸

Ironically, as Riedl argues, it is only because organisms can be classified into distinct groups on the basis of their possession of invariant unique homologs that descent with modification can be inferred in the first place. If it was not for the invariance of the homologs and the Types they define, the very notion of the common descent of all the members of a particular clade from a common ancestor would be in serious doubt. The living realm would conform to a chaotic network rather than an orderly branching tree. (See my discussion of this point in Chapter 6, section 6.1).

Unique invariant homologs which define the Types *do* exist, and it is their retention in invariant form in all the members of the Type they define which not only provides evidence of common descent but is at the basis of all biological classification schemes.

The testimony of a biologist of Riedl’s stature that there are indeed unique Type-defining invariant homologs and that many have been fixed for millions of years is no trivial matter. And Riedl is not alone. Gould similarly acknowledged that “taxonomists must base their hierarchical orderings on nested levels of *homological retention* among related taxa.”³⁹ Someone else who knows the facts is Norman Platnick, Curator Emeritus of the invertebrate zoology department of the American Museum of Natural History. He hit back with a rebuttal to Beatty in *Systematic Zoology* in a letter entitled “Defining Characters and Evolutionary Groups,”⁴⁰ insisting that defining characters do indeed exist and that the typological pattern they imply is compatible with evolution (or, as I prefer to term it, “descent with modification”; see my later discussion in Chapter 6 showing why distinct Types and descent with modification are compatible). In another, earlier landmark

publication Nelson and Platnick defended vigorously the notion that taxa have defining traits and that it is the business of systematics to discover them:

Since the advent of the so-called new Systematics, it has become popular to deprecate as “essentialistic” or “typological” the notions that species (and hence groups of them) have defining characters, and that it is the business of systematics to find them... The rationale for this deprecation seems to be that if evolution occurs, the characters of species (and hence groups) may change in the future; therefore, species and groups of species cannot be permanently characterized by means of a single character or set of characters such that the character or set is necessary and sufficient for membership in the species or group. The argument seems to rest on the misleading use of character states: it assumes that when a species is modified, and acquires a new apomorphic character (state), it is no longer recognizable as having, the original plesiomorphic character (state). In other words, according to this argument, we cannot use characters (such as fins) to define groups (such as Vertebrata), because some members of those groups (such as tetrapods) may acquire apomorphies (such as limbs). If one accepts the validity of ontogeny or outgroup comparison (i.e., Parsimony) or any other possible test of hypotheses about character transformation, the argument is obviated. *In this sense, systematists always have been, are, will be, and should be typologists.*⁴¹

Although the arguments over cladistic methodologies mentioned briefly in Chapter [1](#) may have cooled, the testimony of Colin Patterson, Norman Platnick, Gareth Nelson, Don Rosen, and the other first-class biologists at two of the major biological research institutes in the English-speaking world⁴² still stands: There are taxa-defining novel homologs (the pentadactyl limb, the flower, the diaphragm, etc.); these homologs are not led up to via series of intermediates; and they do persist and exert their constraining powers in diverse lineages in different taxa for millions of years. In other words, typology is no anti-Darwinian fantasy. The testimony of these biologists has left a lasting mark on the evolutionary debate and left Darwinists with an uphill battle trying to perpetrate the illusion that there are no novel taxa-defining homologs in nature.⁴³

Incongruous though it might seem (in the context of the evolutionary propaganda machine and especially to a reader outside of academia), it remains true, as I pointed out in *Evolution: A Theory in Crisis*, that the vast majority of *all* taxa are indeed defined by novelties without any antecedent in any presumed ancestral forms. (See Figure [3-8](#)). The empirical facts make it possible—to paraphrase Dawkins—to be an intellectually satisfied typologist!

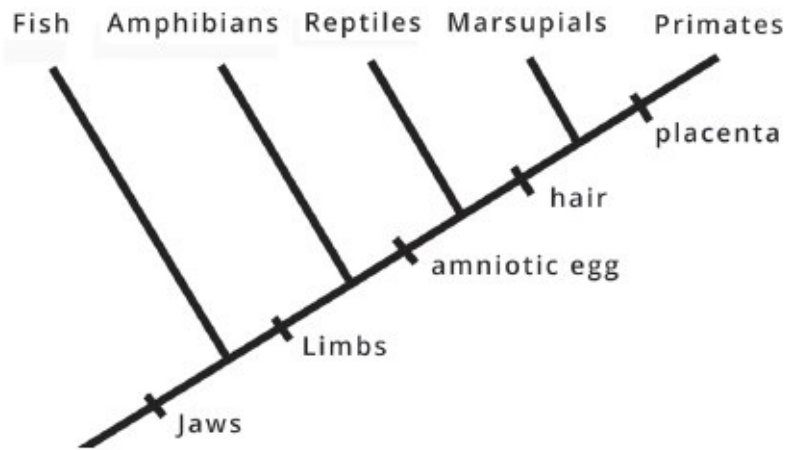


Figure 3-8. Vertebrate Cladogram. Showing the successive acquisition of some of the defining characteristics of modern humans along our phylogenetic lineage.

The near-universal adoption and success in present-day systematics of the cladistic paradigm and its methodology also testifies to typology. The cladistics enterprise would be impossible if different groups were not unambiguously defined by synapomorphies (homologs unique to those particular groups). Indeed, current evolutionary literature is replete with thousands of cladograms to illustrate the phylogeny of various groups of organisms and the sequence in which the various defining traits of the subgroups were acquired.

Types are still as distinct today as they were for Richard Owen, Agassiz, and the other typologists and structuralists in the pre-Darwinian era and even for Darwin himself.⁴⁴ They are still clearly defined by homologs or synapomorphies that are true evolutionary novelties without antecedent in earlier putative ancestral forms. Even in a recent anti-creationist post, the author has to concede: “Importantly, groups are united based on shared ‘derived’ characteristics.”⁴⁵ In other words, groups of organisms are indeed distinguished from each other on the basis of unique sets of defining traits. In effect, all the apomorphies (homologs unique to one particular group) acquired during the course of phylogeny are evolutionary novelties, a point made by Wallace Arthur when he commented: “Novelties and apomorphies are essentially the same.”⁴⁶

3.3 Novelty

That the “gaps” or discontinuities alluded to over and over again in *Evolution: A Theory in Crisis* are real is also attested by the widespread occurrence in current literature of the terms “novelty” and “innovation” and the equally widespread acknowledgment that explaining how novelties come about is one of the major unfinished tasks of evolutionary biology.

Sean B. Carroll, perhaps one of the most committed Darwinists among researchers in evo-devo, gives a section of his lucid *Endless Forms Most Beautiful*⁴⁷ the title “On Novelties” and uses the term “innovation” over twenty-five times in the text. Further, he explicitly describes the ground plan of the butterfly wing, the insect wing, and the autopod (in man the autopod refers to the hand and foot, the distalmost component of the limb) as “innovations.” From his discussion of these and other “novelties,” it is quite clear that he makes no pretense that they are led up to via functional continuums. Even that doyen of

Darwinists, Ernst Mayr, accepted that novelties do indeed exist, and he produced a well-known paper discussing the subject entitled “The Emergence of Evolutionary Novelties” for a conference celebrating the centenary of the publication of *Origin of Species*.⁴⁸

The titles of many recent books and papers in evo-devo and in evolutionary biology generally also betray the fact that genuine novelties are a primal fact of the biological universe.⁴⁹ And as Massimo Pigliucci reminds us, novelties are not restricted to the defining traits of the major phyla: “[Novelties] span all levels of biological organization, from morphological to behavioral to molecular traits.”⁵⁰

Günter Wagner distinguishes two types of evolutionary novelty: those (Type I) without any antecedent (new homologs), and those (Type II) that involve a major character transformation of an existing homolog.⁵¹ This distinction is perfectly valid. However, in the argument I mount here, I am using the term “novelty” or homolog to cover both Type I and Type II novelties, because systematists use both sorts of novelties as defining traits in classifying taxa. Moreover, both sorts of novelty are invariably difficult to account for in terms of Darwinian cumulative selection.

Not only is the existence of genuine novel homologs widely conceded; it is also widely acknowledged that explaining how novelties arise is one of the key problems that evolutionary biology must address.⁵² As Wagner comments: “The most promising areas for developmental evolution [are] the explanation of evolutionary innovations and the evolution of body plans. Indeed, the most exciting research in developmental evolution is directly or indirectly aiming at these questions, which proved to be out of the reach of the classical population genetics.”⁵³ In another recent paper, Wagner and Lynch explain that accounting for the origin of novelties involves a new research program focused “on the evolution of body plans of multicellular organisms” in which “researchers seek to explain the origin of flowers, feathers, and the turtle[']s shell.” They freely admit that “the study of these and other morphological novelties faces unique challenges, among the most important of which is explaining the origin and divergence of the novel gene regulatory networks that give morphological innovations their unique developmental and evolutionary identity.”⁵⁴

Again, Wagner and Lynch acknowledge in another recent article: “A fundamental challenge in biology is explaining the origin of novel phenotypic characters such as new cell types.”⁵⁵ Pigliucci comments in the same vein: “[E]volutionary novelties persist as a fascinating problem for theorists and experimentalists alike, a problem that has been taken seriously enough to become *a major stated goal of a whole field of investigation, known as ‘evo-devo.’*”⁵⁶

In short, nature is still very much an empirical discontinuum of invariant unique forms, and there is no *direct* evidence that the “gaps” were ever closed by the functional continuums demanded by Darwinian theory. The fact that nearly all the authors cited above who confess to the reality of taxon-defining novelties are confirmed evolutionists—and are therefore intellectually predisposed to seek transitional forms—only serves to highlight the fact that the homologs are genuine novelties and the divisions they define are real!

This is not to claim that the Types were not actualized by natural processes. I believe

they were and that the entire pattern of evolution was prefigured into the order of things from the beginning. Although I think the evidence is consistent with most of the novelties being achieved in a relatively saltational manner (as discussed in Chapter 6, section 6.4), typology does not demand absolute saltation, just that the Types (or more properly the homologs which define them) are a special set of robust natural forms or stable material systems, part of nature's order from the moment of creation, to which the paths of evolution were inevitably drawn.

3.4 Summary

In *Evolution: A Theory in Crisis*, I wrote:

The same deep homologous resemblance [novelties/synapomorphies] which serves to link all the members of one class together into a natural group [or clade] also serves to distinguish that class unambiguously from all other classes. Similarly, the same hierarchic pattern which may be explained in terms of a theory of common descent, also, by its very nature, implies the existence of deep divisions in the order of nature. The same facts... which proclaim unity also proclaim division; while resemblance suggests evolution, division, especially where it appears profound, is counter-evidence against the whole notion of [gradual] transmutation.⁵⁷

Thirty years later, despite the discovery of a huge number of new fossil forms and despite massive advances in every field of biology, especially evo-devo, it is still overwhelmingly true, as I insisted in *Evolution* and as Darwin confessed 150 years ago: "The distinctness of specific forms and their not being blended together by innumerable transitional links, is a very obvious difficulty."⁵⁸ Evolutionary novelties do exist and accounting for their causation is one of the major unsolved challenges of evolutionary biology.

Given their distinctness and the general absence of known intermediates leading to the homologs from antecedent structures, given their stunning invariance and constraining powers in so many diverse lineages, subject to all manner of contingencies not for a few years or a few centuries but for in many cases, vast periods of time, periods of time which represent a significant fraction of all cosmic time since the Big Bang, it is small wonder that pre-Darwinian biology saw the homologs as natural forms. How could mere contingent Darwinian assemblages, hobbled together to serve functions at specific times in phylogeny, possess such properties and exhibit such subsequent invariance?

In the next chapter, we will begin to explore the pervasiveness of nonadaptive order in nature and the additional challenge it poses to Darwinian explanations.

4. Non-Adaptive Order

It might have been thought... that those parts of the structure which determined the habits of life [adaptive features]... would be of very high importance in classification. Nothing can be more false... It may even be given as a general rule, that the less any part of the organisation is concerned with special habits [adaptations] the more important it becomes for classification.

Charles Darwin, *On the Origin of Species* (1872), Chapter 14.

At London's famous Natural History Museum in South Kensington, a statue of Richard Owen had been prominently placed for many decades at the head of the main staircase. But in a curiously symbolic event on May 23, 2008, the statue was moved to one of the adjacent balconies to make room for a statue of Charles Darwin, which now sits in pride of place.¹

The reason for this gesture? The Natural History Museum is currently one of the grand temples to Darwinian evolution, and Owen was a staunch defender of the alternative structuralist conception of nature—a conception, which, if true, would relegate Darwinian selectionism to a very trivial role in the evolution of life.

Owen founded the museum and served as its first curator and director. He made huge contributions to comparative anatomy and paleontology in the nineteenth century, including coining the term “dinosaur” and defining the term “homology.” He rejected Darwin's view that the fundamental purpose of any evolutionary theory must be to explain how organisms came to acquire what Darwin called in the introduction of the *Origin* “that perfection of structure and coadaptation which justly excites our admiration.”² On the contrary, Owen believed that there was a substantial degree of order inherent in living systems, manifest in what he termed “primal patterns,” the grand taxa-defining homologs or ground plans that underlie the adaptive diversity of life. Owen argued that many of these ground plans (like the pentadactyl ground plan of the tetrapod limb) do not appear to be adaptive. That is, they do not appear to have or to have ever had any role in fashioning actual organisms to meet specific adaptive ends.³ Such “primal patterns”—transcending “any particular circumstance” as Gould describes it⁴—therefore could not be the result of adaptive evolution as Darwin claimed. Owen believed, as mentioned in Chapter 1, that these deep homologous patterns were immanent aspects of the world order which arose in some way from the intrinsic physical properties of living things.

Because of his vigorous opposition to the functional conception of nature, Owen was vilified by Thomas Huxley and other supporters of Darwin. After the publication of the *Origin*, Owen's contribution to biology was increasingly downplayed by the Darwin camp, and his rejection of the conception that all biological order was to “serve some utilitarian end” was dismissed as archaic and treated as based on failed metaphysical assumptions. Little wonder they decided to move his statue!

4.1 On the Nature of Limbs

The challenge posed to the Darwinian paradigm by the novelty and uniqueness of the

taxa-defining homologs—and by the absence of *any* evidence they were actualized gradually via transitional sequences—is greatly increased by the fact that in many cases, their adaptive status has never been confirmed or is very much in doubt. To show that their adaptive status is indeed very much in doubt was the grand aim of Owen’s classic critique of functionalism in his landmark *On the Nature of Limbs*, which originated as a lecture before the Royal Institution in Great Britain.⁵ At the beginning of this classic, still one of the greatest anti-functionalist and anti-Darwinian documents ever composed in the English language, Owen makes a remark that has proved to be extraordinarily prophetic:

It was not until I had written and erased two or three [titles for this lecture]... that I became fully conscious how foreign to English philosophy were those ideas or trains of thought [i.e., the structuralist notion that not all aspects of morphology serve functional/adaptive ends] concerned in the discovery of anatomical truths, one of which I propose to explain on the present occasion in reference to the limbs or locomotive extremities.⁶

How true these words have proved to be with English-speaking biologists! That adaptation might *not* be the most fundamental organizing principle in biology, that there might be a substantial amount of order in biological systems that can never be reduced to externalist function-alist explanations, is still for most Anglophone biologists “a bridge too far,” leading to the dark and threatening realm of Continental *naturphilosophie*, German idealistic morphology, and to alien figures such as Lorenz Oken and Goethe. As Gareth Nelson laments, the deep insights of such thinkers are usually dismissed as “romanticism” in the Anglophone world.⁷ Riedl expressed a similar view in his *Order in Living Organisms*:

In central Europe it has been believed that structural patterns could not be explained entirely in terms of immediate function; and the search for a deeper explanation, which began with Goethe and continued throughout the nineteenth century, became confused with German idealistic philosophy—a fact which made it both difficult and suspect for English speaking scientists... As a result the word ‘morphology’ became disreputable in English.⁸

That the thinking of the continental structuralists cannot be so easily dismissed was conceded in later years by Gould (as mentioned in Chapter [1](#)) and was shown in an important and sympathetic review of Goethe’s concept of the Types by philosopher Ron Brady.⁹

Owen opens *On the Nature of Limbs* by referencing the fin of the dugong, the leg of the horse, the forelimb of the mole, and the wing of the bat in order to show the very different types of adaptation that vertebrates utilize for locomotion in water, on the land, inside the earth, and in the air. He then shows, by illustrations of the individual skeletal designs, that these different limbs are all based on an underlying homologous *Bauplan*—the pentadactyl limb. As he comments: “Such are some of the more striking amongst the countless purposes to which the parts of animals called ‘limbs’ are adapted.” Owen adds that “We cannot be surprised at this; it could not be otherwise: the instrument must be equal to its office.”¹⁰

But what is very surprising is this: If the sole organizational principle of life is (as

functionalists assert) adaptation, why should the adaptive forms of tetrapod limbs—what Owen terms “adaptive masks”—be based on the *same* underlying “primal pattern”? The problem for functionalists is that the underlying pattern cannot itself be construed to be serving any specific adaptive function—i.e., to fit any conceivable *real* organism to any conceivable *actual* environment. As Amundson succinctly comments: “Limbs are differently adapted, but they share common structure. His [Owen’s] point is that the commonality of structure is *not* traceable to function.”¹¹

As Owen points out, mankind does not construct various machines for diverse purposes on the same underlying plan:

To break his ocean-bounds the islander fabricates his craft, and glides over the water by means of the oar, the sail, or the paddle-wheel. To quit the dull earth Man inflates the balloon, and soars aloft, and, perhaps, endeavours to steer or guide his course by the action of broad expanded sheets, like wings. With the arched shield and the spade or pick he bores the tunnel: and his modes of accelerating his speed in moving over the surface of the ground are many and various. But by whatever means or instruments Man aids, or supersedes, his natural locomotive organs, such instruments are adapted expressly and immediately to the end proposed. He does not fetter himself by the trammels of any common type of locomotive instrument, and increase his pains by having to adjust the parts and compensate their proportions so as best to perform the end required... There is no community of plan or structure between Stephenson’s locomotive engine and Brunel’s tunnelling machinery: a very remote analogy, if any, can be traced between the instruments devised by man to travel in the air and on the sea, through the earth or along its surface.¹²

And then Owen makes the decisive point:

Nor should we anticipate, if animated in our researches by the quest for final causes [the adaptational paradigm] in the belief that they were the sole governing principle of organization, a much greater amount of conformity in the construction of the natural instruments by means of which those different elements are traversed by different animals. The teleologist [adaptationist] would rather expect to find the same direct and purposeful adaptation of the limb to its office as in the machine. A deep and pregnant principle in philosophy, therefore, is concerned in the issue of such dissections, and to these, therefore, I now pass, premising that the end in view will be attained without extending the comparison beyond the framework of the limbs, or the leverage of the bones and joints.¹³

Owen again stresses near the end of the monograph: “The Fallacy [of pan-adaptationism] perhaps lies in judging created organs by the analogy of man made machines.”¹⁴

Analogies are hard to come by to illustrate the relationship between the non-adaptive “primal pattern” and the derived “adaptive masks,” and to highlight the non-adaptive and abstract nature of the “primal pattern” itself. A very crude analogy is to think of the “primal pattern” as a fashion designer’s initial drawing to illustrate the design of a new

article of clothing. In itself this “primal pattern” or template is not fit for any particular individual—like the pentadactyl pattern of the limb, which serves no specific adaptive purpose in any specific individual species. The tailor then takes the “ideal pattern” and fashions it in slightly different ways to produce articles of clothing fit for different people. All suits are based on the same underlying design (analogous to the pentadactyl pattern), but each suit also differs in adaptive ways (analogous to the adaptive masks, fins, limbs and wings).

Within the Darwinian worldview, we may see the tailor’s work as analogous to natural selection shaping or adapting the original design (the primal pattern) to fit a specific individual. But the fashion designer’s original “primal pattern” cannot be accounted for in the same way because the design is not fit *for any specific individual*. The initial drawing is an abstract non-adaptive pattern, which only becomes adaptive when the tailor converts the idea into the material form of a particular suit.

As mentioned in Chapter [1](#) and throughout the book, I am using the term non-adaptive to describe any characteristic of an organism that is not for any specific adaptive end. It is important to note that the central point of contention between structuralism and functionalism is *not that primal patterns serve no purpose* (they do “function” as general ground plans upon which adaptive forms are derived), but that they *do not serve, nor have they ever served* to adapt specific organisms to meet specific adaptive ends. That is Owen’s point. They transcend any functional particular! Such patterns, Owen might have argued, could only have arisen from internally imposed constraints or causal factors such as his polarizing force.

Although *Limbs* is, as the title implies, focused on the limb “primal pattern” or *Bauplan*, Owen did not restrict his argument to the *Bauplan* of the limb. He makes it clear that he is using the tetrapod limb to illustrate a general principle that in many cases the homologous commonalities of structure underlying the adaptive diversity of life do not appear to serve any conceivable *specific* adaptive end. To generalize his point, he alludes to the number of bones in the skull of the human fetus and their benefit for safe parturition:

Such a final purpose is indeed readily perceived and admitted in regard to the multiplied points of ossification of the skull of the human foetus, and their relationship to safe parturition. But when we find that the same ossific centres and in similar order are established in the skull of the embryo kangaroo, which is born when an inch in length, and in that of the callow bird that breaks the brittle egg, we feel the truth of Bacon’s comparison of ‘final causes’ to the Vestal Virgins, and perceive that they would be barren and unproductive of the fruits we are labouring to attain, and would yield us no clue to the comprehension of that law of conformity [the unity of the Type] of which we are in quest.¹⁵

Darwin was clearly impressed by Owen’s critique of pan-adaptationism in *Limbs*. In the *Origin* he concedes:

What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the

wing of the bat, should all be constructed on the same pattern, and should include similar bones, in the same relative positions? How curious it is, to give a subordinate though striking instance, that the hind-feet of the kangaroo, which are so well fitted for bounding over the open plains,—those of the climbing, leaf-eating koala, equally well fitted for grasping the branches of trees,—those of the ground-dwelling, insect or root-eating, bandicoots,—and those of some other Australian marsupials,—should all be constructed on the same extraordinary type, namely with the bones of the second and third digits extremely slender and enveloped within the same skin, so that they appear like a single toe furnished with two claws. Notwithstanding this similarity of pattern, it is obvious that the hind feet of these several animals are used for as widely different purposes as it is possible to conceive. The case is rendered all the more striking by the American opossums, which follow nearly the same habits of life as some of their Australian relatives, having feet constructed on the ordinary plan.¹⁶

We see the same great law in the construction of the mouths of insects: what can be more different than the immensely long spiral proboscis of a sphinx-moth, the curious folded one of a bee or bug, and the great jaws of a beetle?—yet all these organs, serving for such widely different purposes, are formed by infinitely numerous modifications of an upper lip, mandibles, and two pairs of maxillæ.¹⁷

Darwin actually concedes that these formal patterns have no apparent specific adaptive utility: “Nothing can be more hopeless than to attempt to explain this similarity of pattern of members of the same class, by utility [to serve environmental constraints] or by the doctrine of final causes [teleology or design]. The hopelessness of the attempt has been expressly admitted by Owen in his most interesting work on the ‘Nature of Limbs.’”¹⁸ Darwin also specifically mentions Owen’s allusion to multiple centers of ossification in the vertebrate skull as being beyond adaptive explanation: “As Owen has remarked, the benefit derived from the yielding of the separate pieces in the act of parturition by mammals, will by no means explain the same construction in the skulls of birds and reptiles.”¹⁹

Owen’s conclusion was simple and compelling: Functionalism cannot provide a comprehensive explanation for *all* organic order, and adaptation is not the only or even the primary organizational principle of biology.²⁰ Whatever else *Limbs* achieved, it rendered pan-adaptationism absurd. As Amundson comments: “Owen didn’t just ‘admit’ the failure of teleology [pan-adaptationism] ... in *Limbs*: he gleefully proved it!”²¹

Of course, along with all other nineteenth-century structuralists, Owen had no idea of exactly what internal constraints or laws might be involved in generating the homologs and what conferred upon them their remarkable, active, constraining influence in diverse lineages for hundreds of millions of years. Like many other pre-Darwinian biologists (see Chapter 1), he believed that the homologs were analogous to natural forms like crystals and arose though the activities of as-yet-undefined “laws of form” (his “polarizing force”) and which as genuine universals might operate on other life-bearing planets generating forms of life similar to those now existing on earth. Although, as Dov Ospovat comments, Owen saw that “the Goal of the comparative anatomist... is to discover the laws

governing this conformity to pattern [the unity of the Type],”²² Owen concedes in the last paragraph of *On the Nature of Limbs* that the precise nature of those laws remained elusive.²³

It is important to note that although Owen rejected the notion that the homologs like the *Bauplan* of the limb could be explained in terms of design to serve some *specific* adaptive end, he very definitely did *not* reject the notion that the *Bauplans* themselves are the result of design or that nature exhibited evidence of design. Indeed, on the contrary he argued that the underlying primal patterns/archetypes reflected an overall transcendent purpose of the Divine mind. He even suggested that this transcendent purpose was to lead eventually to the development of mankind: “Now... the recognition of an ideal Exemplar for the Vertebrated animals proves that the knowledge of such a being as Man must have existed before Man appeared.”²⁴ As mentioned in Chapter 2, Owen also spoke of “a predetermining Will, producing [living forms] in reference to a final purpose” in the preface of his *On the Anatomy of Vertebrates*.²⁵

Thus, Owen’s critique of teleology did not involve denial of the notion that nature manifests evidence of design. Owen’s critique of panadaptationism is perfectly compatible with the idea that the universe and life reflect an intelligent design. But Owen’s critique is most definitely *not* compatible with the classical Darwinian pan-adaptational view, which implies that every feature of every living thing is, or once was in some ancestral form there to serve some specific adaptive end.

Nicolaas Rupke notes that Owen’s conception of the archetype or *Bauplan* did shift the evidence for design from special to general teleology: “Divine contrivance was to be recognized not so much anymore in the characteristics of separate species but in their common ground plan. God was no longer the Supreme Watchmaker but the Supreme Architect, who had personally conceived the blueprint of nature, yet employed natural laws for the actual construction work.”²⁶

In this context, it is worth considering Owen’s belief that the laws of nature are fully capable of doing God’s “constructional work” in actualizing design in nature. Consider the example of water. No one will deny that water exhibits myriads of adaptive features—including its various thermal properties, its solvation properties, its viscosity, its erosional properties, and so forth—which fit it perfectly and ideally to form the matrix of life on earth. But neither will anyone dispute the claim that water is the product of entirely natural processes. For example, no one doubts that the formula H₂O—two hydrogen atoms combined with one oxygen atom—is determined by the electronic structure of the hydrogen and oxygen atoms. No one doubts that the synthesis of the atoms of the periodic table including oxygen occurs by nuclear synthesis in stellar interiors and are scattered throughout the cosmos when stars die either sedately or in a supernova. No one doubts that the hydrogen atoms [H] were generated, also by nuclear synthesis but in the first few minutes following the creation of the universe. And no one doubts that wherever oxygen and hydrogen atoms are in contact at temperatures below several thousand degrees, two atoms of hydrogen combine with one atom of oxygen.

So water, which exhibits a suite of extraordinary adaptive features, perhaps more than any other entity in nature—no gene and no protein can compete with water in serving so many diverse adaptive ends—is indeed the product of natural law. (See also my

description in Chapter [13](#) [section 13.4] of the various forms that water can adopt as further evidence of the power of natural law to generate complex material forms.) If the wondrous adaptive fitness of water is deemed to be the result of design—as many would argue—then there would seem to be no design which is beyond the “constructional reach” of natural law. Although Owen was at times accused of materialism^{[27](#)} because of his advocacy of *nomogenesis* (life arising by natural law), if materialism is taken to imply that matter is *all* there is and that the laws of nature have arisen fortuitously from the *blind* concourse of atoms in motion, then Owen was certainly no materialist. He saw the laws of nature and the properties of matter as bearing the impress of a Divine purpose—namely, to generate the realm of life as manifest on earth.

4.2 Numerics and Geometrics

While many of the taxa-defining homologs—including, among others, the feather, the poison claw of the centipede, the retractable claw of cats, the mammalian diaphragm, and mammary glands—are clearly adaptive, a great many others (e.g., the odd number of segments in centipedes, the concentric whorls of the flower, and the insect body plan)—convey the powerful impression of being like the pentadactyl “primal pattern,” basically non-adaptive *Bauplans*. The fact that many exhibit curious geometric and numeric features reinforces the impression that they are indeed abstract non-adaptive patterns, quite beyond the explanatory reach of any adaptationist or selectionist narrative.

Consider the following numerical examples. Nearly all mammals have *seven* cervical vertebrae.^{[28](#)} And, as mentioned above, all mammals have *six* distinct layers of cells in their cerebral cortex. Again, as we saw above, all insects are divided into *three* main body segments: head, thorax, and abdomen. Their legs have *five* divisions. Again, all Longicornia beetles have *eleven* joints in their antennae, except one small subgroup (the Longicorn Prionidae), most of which have the unusual number of *twelve* antennary joints.^{[29](#)} All *Drosophila melanogaster* fruit flies have *twenty* pairs of bristles on their back, all placed in precisely the same geometric position in every individual fruit fly.^{[30](#)}

Consider the geometrics of the wing venation patterns of particular groups of insects. In the case of the Nymphalid butterflies, the curious geometry includes the following elements as described in Charles Bingham’s classic text on the butterflies of south Asia:

Fore wing: submedial vein or vein 1, simple, in one subfamily forked near base; medial vein with three branches, veins 2, 3, and 4; veins 5 and 6 arising from the points of junction of the discocellulars; subcostal vein and its continuation beyond apex of cell, vein 7, with never more than four branches, veins 8–11; 8 and 9 always arising from vein 7, 10, and also 11 sometimes from vein 7 but more often free, i.e., given off by the subcostal vein before apex of cell.^{[31](#)}

What adaptive function can such extraordinarily complex highly conserved abstract patterns serve?

The texts of invertebrate paleontology are full of homologous “numerology and geometrics.” Robert Schrock and William Twenhofel’s classic *Principles of Invertebrate Paleontology*^{[32](#)} has examples on nearly every one of the 781 pages of the text. For example, the number of segments making up the various parts of the body of different groups of arthropods—shrimps, lobsters, trilobites, spiders and so forth—is fantastically

variable, yet each group almost always has the same number of segments in each body part despite the bizarre and complex variation in life style and adaptations.³³ To this I would add the following observations, which I presented in slightly different words in a previous paper.³⁴

Among the cephalopods, the octopi (order Octopoda) have eight tentacles of similar length, while the squids (Teuthoidea) have ten, two of which are considerably longer than the other eight.³⁵ Again, octopi and squids have two gills, while other cephalopods, including the nautilus, have four. The starfishes and sand dollars (Echinodermata) exhibit a pentamerous or fivefold symmetry.³⁶ Among the jellyfishes, sea anemones, and corals (Cnidaria), there are a great variety of intriguing radial symmetries.³⁷ The jellyfishes (Scyphozoa) usually exhibit a tetramerous or fourfold symmetry, “having their parts symmetrically repeated round their mouth to feet axis [oral aboral axis] to the number 4 or multiples of 4”; however, some species “are built on a plan of 6, and have a hexamerous symmetry.”³⁸ Again, among the sea anemones and related polypoid forms (Anthozoa), different classes are differentiated by different types of radial symmetries and can be classified by number and arrangement of tentacles and mesenteries and number and arrangement of septa.³⁹ One colonial subclass (Alcyonaria) possesses eight pinnate tentacles forming a marginal circle on the oral disc and eight mesenteries attached to the gullet: “The eight symmetrically arranged tentacles and mesenteries give the polyp what seems to be an octamerous radial symmetry.” Another subclass of sea anemones (Zoantharia) is subdivided into a variety of groups exhibiting a complex sixfold symmetry with “mesenteries in cycles of 6, 12 or multiples of 6.”⁴⁰

On even a cursory consideration of the vast universe of Type-defining novelties, it would appear that a significant fraction exhibit numerical patterns which serve no specific adaptive purpose. And in all those cases Darwinian explanations based on functionalist adaptive scenarios are simply ruled out of court. The difficulty of accounting for such arbitrary geometric and numerical patterns in terms of bit-by-bit selection was one of the basic thrusts of William Bateson’s vigorous attack on Darwinian orthodoxy. In his *Materials for the Study of Variation*, he sarcastically comments:

Would it be expected that the longicorn Prionidae, most of which have the unusual number of 12 antennary joints, did, as they separated from other longicorns which have 11 joints, gradually first acquire a new joint as a rudiment which in successive generations increased?... If anyone will try to apply such a view to hundreds of like examples in arthropods, of difference in number of joints and appendages of near allies... he will find that by this supposition of continuity in variation he is led into endless absurdity.⁴¹

In another passage, Bateson comments: “It is scarcely necessary to point out that these facts give no support to the view that the exactness or perfection with which the proportions of the normal form are approached is a consequence of Selection [for biological function].”⁴²

If indeed a significant proportion of the taxa-defining primal patterns serve no specific adaptive function and never did, as common sense dictates and as Owen clearly thought to be true of the *Bauplan* of the tetrapod limb, then I think a fair assessment has to be that Darwinism (more specifically, cumulative selection) *cannot supply an explanation*

for the origin of a significant fraction of the defining homologs of the Types and hence for the natural system itself.

4.3 Darwin's Legitimation

To save his functionalist worldview, Darwin made what must be judged as one of the most unjustified legitimations in the history of science—the claim that many of the homologs that define the Types, which as we saw above he concedes have no conceivable utility in extant organisms, represent “leftovers,” or as Amundson describes them, “residues of evolution”—ancient adaptations no longer useful but incorporated into the genetic system and passed down through the generations.⁴³

This is surely one of the most remarkable examples of what Nagel terms “a heroic triumph of ideological theory over common sense,”⁴⁴ and of “looking away” from the actual empirical evidence.⁴⁵ Darwin gave the “leftover” legitimation for persistent homologous pattern in many places in *On the Origin of Species*. Here are some sample passages:

The chief part of the organisation of every living creature is due to inheritance; and consequently, though each being assuredly is well fitted [adapted] for its place in nature, many structures [the underlying homologs] have now no very close and direct relation to present habits of life... [W]e cannot believe that the similar bones in the arm of the monkey, in the fore-leg of the horse, in the wing of the bat, and in the flipper of the seal, are of special use to these animals. We may safely attribute these structures to inheritance.⁴⁶

If we suppose that an early progenitor—the archetype as it may be called—of all mammals, birds, and reptiles, had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the class.⁴⁷

Clearly, Darwin's “explanation” that the homologs once served some purpose in some hypothetical ancestral form that he cannot specify is just an *ad hoc* legitimation.⁴⁸ Of course, it is an essential rationalization if Darwinism is to have any shred of credibility. But nowhere in the *Origin* does he attempt to provide any significant justification for this radical claim. He does not show, for example, that five fingers were the adaptive response to some environmental constraint in the ancestral tetrapod ancestor, that the same design in fore and hind-limbs served some environmental constraint in some obscure ancestral amphibian, or that the three thoracic segments were adaptive in the “ancestral insect.”⁴⁹ Indeed, to show that the vast universe of apparently abstract and non-adaptive *Bauplans* and homologs were *once upon a time* adaptive, once upon a time fashioned by some environmental constraint to serve some functional end, especially given the curious numeric and geometric characteristics that so many exhibit, poses a Herculean challenge to the entire function-alist framework.

Darwin, as is well known, appealed to common descent to explain the fact that all the members of a clade possessed the same suite of defining homologs. But even if common descent might explain the fact that all mammals possess hair or that all birds possess feathers, appealing to common descent does not provide a causal explanation of *how the*

patterns originated in the first place in the “ancestral form.” Darwin and subsequent Darwinists are wrong—dead wrong—to assume that the common inheritance of the homolog from a common ancestor somehow provides a causal explanation for the origin and emergence of the homolog itself and of the Type it defines. Common descent may explain why all members of a clade share a homolog, but not that the homolog was adaptive in the common ancestor.⁵⁰

If Owen is right about the ontological status of many of the major *Bauplans* as fundamentally non-adaptive ground plans (and there is no contrary evidence), there is no possibility of accounting for their origin in terms of Darwinian incremental functionalism. If Darwin had fully grasped Owen’s point that only the “adaptive masks” built upon the *Bau-plans*, but not the *Bauplans* themselves, are adaptations to meet specific environmental constraints—or, at least, if Darwin had understood that there is no evidence that the homologs had ever served adaptive functions—he never would have claimed that they were adaptive in hypothetical ancestral forms, and I believe he might never have written the *Origin of Species*.

The *Origin* is based, I believe, on a fundamental misinterpretation of the nature of the homologs, on a basic failure to grasp the challenging implication of Owen that there are no grounds for believing that “primal patterns” like the limb or insect *Bauplan* ever fashioned a particular (real) organism to meet a particular (real) functional end. In other words, the *Origin* effectively ignores the profoundly subversive fact that a great deal of order in living organisms has never been shown to be adaptive either in extant or in ancient forms.

No matter how many times Darwinists reiterate the fairy story that the homologs were “once upon a time” adaptive in the ancestor of the clade they define, it is a claim without the slightest empirical or rational basis. Step outside the circle of pan-adaptationist belief and the nature of the claim as pure legitimation is only too painfully obvious. Indeed, so damning to the Darwinian enterprise is the failure to explain in externalist functionalist terms the universe of underlying “primal patterns” that all other critiques of Darwinism are in effect rendered superfluous. The existential nature of Owen’s challenge to Darwinian functionalism is now apparent. It can hardly be exaggerated. If Owen is right and the apparently non-adaptive *Bauplans* which underlie the adaptive diversity of life are indeed non-adaptive, then the whole Darwinian edifice stands on sand, on an unproven assertion which can never be finally proved, and which seems exceedingly unlikely to be true.

In the last analysis, whatever might turn out to be the causal explanation of the taxa-defining novelties—whether they are indeed generated by “laws of form” as I believe many are, and as many patterns in the natural world such as radiolarian shells and the number of petals in particularly species of daisy undoubtedly are—there is no question that neither Darwin nor any subsequent Darwinist has provided any convincing justification for their *a priori* functionalism.

4.4 A Universe of Non-Adaptive Forms

A majore problem in defending the Darwinian claim that the apparently non-adaptive homologs, are (or were once) adaptive structures serving some elusive environmental

constraint is the existence of a vast universe of non-adaptive forms and patterns in nature which no biologist—not even the most convinced functionalist or Darwinist—has ever viewed as adaptive. This raises an obvious problem: On what *objective* grounds can homologous patterns like the pentadactyl limb or the concentric whorls of the angiosperm flower be differentiated from the host of patterns, some of which are exceedingly complex, which no one doubts are abstract, a-functional patterns?

In a previous article, I wrote:

To take one example, the shells and tests of unicellular organisms, including radiolaria, foraminifera, and diatoms, display a bewildering universe of diverse forms, some highly geometric but others as abstract as a Kandinsky painting... That many of these forms are abstract structures produced by the direct action of physical law, no less than the generally round shape of a cell, was wonderfully argued in D'Arcy Thompson's *On Growth and Form*: "The forces that bring about the sphere, the cylinder or the ellipsoid are the same yesterday and tomorrow. A snow crystal is the same today as when the first snows fell. The physical forces which mold the forms of *Orbulina*, of *Astrorhiza*, of *Lagena* or of *Nodosaria* today were still the same, and for aught we have reason to believe the physical conditions under which they worked were not appreciably different, in that yesterday we call the Cretaceous."⁵¹

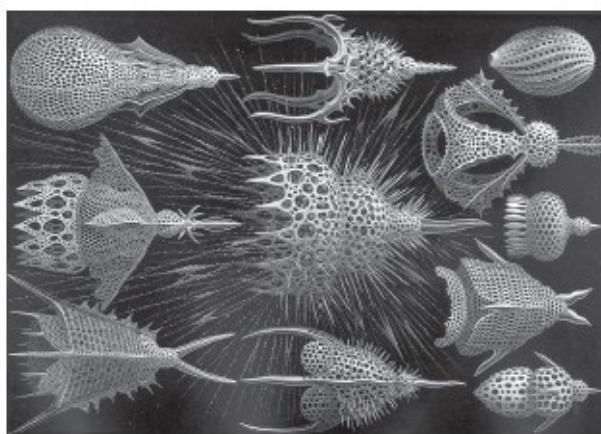


Figure 4-1. Radiolarian Shells.

It is not only the unicellular world that abounds with what appear to be abstract formal patterns. Even on the most cursory and passing observation of some of the most familiar natural forms, such as the forms of leaves and the variety of phyllotactic arrangements that might be observed in any suburban garden, it is hard to resist concluding that a vast amount of botanical order serves no specific adaptive end. Take the different number of petals on different species of flower. In many species the number of petals often corresponds to a Fibonacci number, e.g., bloodroot, eight; blackeyed daisy, thirteen; shasta daisy, twenty-one; and field daisy, thirty-four.⁵² Would anyone seriously insist that the number of petals in each species is adaptive?



Figure 4-2. Maple Leaf.

In the context of what appears to be a veritable universe of nonadaptive form permeating all nature, acknowledged universally by all biologists of every hue, the Darwinian claim that all the apparently nonadaptive *Bauplans* and taxa-defining homologs were actually adaptive in ancestral forms is self-evidently *ad hoc*, a necessary presumption pulled out of the air to justify the Darwinian paradigm. If it is universally accepted that the pattern of daisy petals serves no specific adaptive purpose (i.e., confers no enhancement of fitness in any conceivable environment), then why could this not be true also of the grand homologies? The reason is all too obvious. If the pentadactyl limb or the insect *Bauplan* are also a-functional patterns, like the thirty-four petals of a field daisy or the shape of a maple leaf, then *the whole Darwinian enterprise breaks down*. Darwinism would be insignificant, reduced to explaining the beak of the finch but not the limb of the tetrapod. The grand fact of what appears to be a veritable universe of biological order, order which has never been shown to be adaptive, is the *nemesis*, the very Achilles heel, of the whole functionalist tradition. No wonder they moved Owen's statue!

4.5 The Enigma of Fixation

The failure to demonstrate their utility to serve adaptive ends is by no means the end of the challenge to Darwinian orthodoxy in accounting for the origin and fixation of the grand ground plans in functionalist terms.

Let us allow, for the sake of argument, that the evolution of the form of a homolog, say the pentadactyl limb design, came about in Darwinian fashion via incremental adaptive steps so that a fin gradually changed into the canonical tetrapod pentadactyl limb and that these intermediate forms were adaptive in the immediate environments in which the transitional forms lived. Common sense dictates in such a scenario that during its evolution the form of the fin/limb must have been fluid for millions of years while the form of the limb was gradually emerging in the late Devonian era. And if this is the case, we must assume that the fin or limb progenitor was a module able to undergo change, free from constraints imposed by the integrative complexity of the pre-existing body plan of the lobe-finned fish.

But this explanation leads to further problems. If the homolog was “fluid” during the transition, why and how did it become fixed when the pentadactyl pattern finally emerged? Why should the canonical form have any special significance? What adaptive forces fixed a previously fluid pattern at a particular moment in evolutionary time? If adaptation can change one structure, the fin, why not its successor, the limb? The fixation of the pattern underlying all the adaptive modifications in diverse lines over the next 400 million years is all the more curious considering that the adaptive forms based upon the *Bauplan* did indeed change. What isolated the *Bauplan*—the one, two, five, pattern—from

its adaptive masks, imposing absolute invariance against any evolutionary change, while permitting vast evolutionary change in all the derived forms (the adaptive masks)? Self-evidently the initial fixation cannot be explained plausibly in Darwinian terms.

Of course, the problem is not restricted to the pentadactyl limb. All the homologs must also have undergone the utterly un-Darwinian transformation from “evolvable” to “immutable.” The insect body plan, the whorled pattern of the flower, the eleven antennal segments of beetles, the venation patterns of insect wings, the left-right symmetry of bilateral animals, and so on *ad infinitum*. As they “evolved,” all these deep homologous patterns must have once been *variable* and served mysteriously obscure adaptive functions (for which there is not the slightest evidence) and then they subsequently became invariable from the point when they no longer served any specific adaptive function.

There is simply no way that fixity or invariance of any organic structure can ever be conceived to be adaptive in a world of ever-changing environmental contingencies. Would there be any advantage to a species of Galápagos finch in fixing its beak form for all subsequent evolutionary time? Such fixity would be profoundly non-adaptive.

4.6 Exaptation and Spandrels

I will add a word here about two functionalist proposals offered by Darwin for the origin of evolutionary novelties. The first proposal was that novel traits could arise because of what Gould calls “functional change with structural continuity” or exaptation.⁵³ The commonly cited example is that of feathers, which, it is argued, were first evolved for temperature regulation and later co-opted for flight. Another example might be the evolution of the swim bladder—a buoyancy control organ—in teleost fishes, derived from the lungs of more primitive ancestral fishes.

The problem is that while functional co-option may account for a new functional adaptation of a pre-existing structural feature, it cannot account for the *actualization* of any novelty where there is no antecedent structure or where there is no functional continuum or where the novelty appears to serve *no obvious adaptive function*, which seems to be true in the case of many, perhaps the majority, of the *Bauplans* and many of the taxa-defining homologs. (As will become clear on the detailed consideration of the origin of novelties in future chapters, the great majority of novelties such as the feather, the tetrapod limb, the angiosperm flower, etc. cannot be explained in terms of “functional shifts.”)

Darwin’s other proposal, alluded to above, was that non-adaptive novelty might arise as the unintended but inevitable by-product of selection for some entirely unrelated trait. Such novelties Gould termed “spandrels” (borrowing the term used to describe the space between an arch and a rectangular enclosure in the architecture of cathedrals).⁵⁴ As Darwin explained: “If man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation.”⁵⁵ Gould cites the classic example of the empty cylindrical space—the umbilicus—which arises inevitably from the way snails build their shells, by winding a tube around an axis of coiling, an empty space of no direct adaptive utility to the snail.⁵⁶ Might non-adaptive homologs have originated as spandrels? Such a possibility could only be taken seriously if (as in the case of the umbilicus) plausible scenarios can be envisaged.

However, in the case of the great majority of novel homologs, such as the flower or the limb designs of insects and vertebrates, *no one has ever proposed plausible selection pressures that might have operated for hundreds of millions of years in diverse lineages to maintain the form of the homolog.*

It is important to note that Darwin himself never claimed that these two proposals for the origin of novelty applied to the major taxa-defining *Bauplans* such as the pentadactyl limb or the angiosperm flower.

4.7 Confession

If, in *Evolution: A Theory in Crisis*, I had followed Owen, and pointed out that many of the defining homologs and *Bauplans* have never been shown to be specifically adaptive, it would have very greatly reinforced my critique. Although I read Gould's "Spandrel paper" several years before *Evolution* was published, and although I had been puzzled at King's College regarding the apparently non-adaptive enucleate red cell (see detailed discussion in Chapter 7), I was still basically a functionalist in 1985.

To be sure, the puzzle of homology was apparent even at medical school in Bristol, where the homologous structure of the hand and foot were obvious in the dissection room, and alluded to by David Yoffe, the then Professor of Anatomy.

But more than any other individual, it was Marcel-Paul ("Marco") Schützenberger who started me on a thirty-year road to structuralism, by pointing out the abstract appearance of so many botanical forms during several visits to the Jardin de Plantes in Paris in the late 1980s.

I am somewhat embarrassed by my late discovery of the structuralist tradition and my failure to see through the pan-selectionist mirage to the deep layer of a-functional order which permeates living things, but I am in good company. Even Gould admitted to being "embarrassed by the fervor of [the] adaptationist convictions" he held early in his career, before he came to realize the significance of the structuralist tradition and the challenge it posed to the Darwinian framework.⁵⁷ Gould wrote:

Finally, if I could... wipe any of my publications off the face of the earth and out of all memory, I would gladly nominate my unfortunately rather popular review article on "Evolutionary paleontology and the science of form"... a ringing paean to selectionist absolutism, buttressed [by the idea that one] could... prove panadaptationism even for fossils that could not be run through the hoops of actual experiments.⁵⁸

As I pointed out earlier, Gould described his appreciation later in his career for continental structuralist thought and for its "sheer intellectual power."⁵⁹

4.8 Summary

In this chapter, we have seen that further undermining the Darwinian account of evolution is the fact that a great deal of organic order appears to be non-adaptive. This includes a great number of the taxa-defining *Bauplans*, such as the pentadactyl limb, the flower, the pattern of insect wing venation, and so forth. These *Bauplans* give not the slightest impression, nor is there any evidence for believing, that they serve in extant organisms, or

ever did serve in extinct forms, any specific adaptive function, i.e., fitted actual species to actual environments. They therefore could not have originated as a result of gradual Darwinian adaptive evolution.

In the next chapter, we will examine the discoveries associated with the new field of evo-devo and see how these discoveries have undermined the Darwinian model as well.

5. Evo-Devo

Important changes in the embryo or larva will probably entail changes in the mature animal. In monstrosities, the correlations between quite distinct parts are very curious; and many instances are given in Isidore Geoffroy St. Hilaire's great work on this subject.

Charles Darwin, *On the Origin of Species* (1872), Chapter 1.

One of the major advances since *Evolution: A Theory in Crisis* has been the revolutionary increase in our understanding of development and especially the genetics of development,¹ about which little was known in 1985. These new advances in genetics and developmental biology have led to the emergence of a whole new field, nicknamed “evo-devo” (evolutionary developmental biology). At the heart of these advances has been the discovery that a limited set of highly conserved genes, gene circuits, and developmental mechanisms—*Hox* genes, signaling proteins such as “sonic hedgehog,” chemical gradients, and gene regulatory networks, referred to by Davidson and Erwin as “kernals”²—are involved in the construction of the bodies of all bilaterally symmetric animals,³ all the morphological homologs, and indeed of all higher organismic form. Sean Carroll has termed this set of conserved genes and developmental mechanisms the “toolkit.”⁴

Before these evo-devo revelations distantly related groups (e.g., insects and vertebrates) were thought to have no shared genes or developmental processes except very basic biochemical and molecular features (e.g., the core metabolic pathways, the genetic code, the roles of DNA and RNA, and the basic design of the cell). But now we know that the developmental genetic commonalities run very deep. One of the most remarkable discoveries in this field was the dramatic finding that in both *Drosophila* and humans, mutations in the same gene, *Pax6*, causes mal-development of the eye. It is now known that *Pax6* turns on the genetic circuitry which leads to the development of the eye in a vast range of animals, even though the eyes, such as those of insects, vertebrates and cephalopods (squid) could hardly be more different in fundamental design.⁵

Even more remarkable was the discovery that in a vast diversity of bilaterally symmetrical (bilaterian) animals (including insects and vertebrates) the linear order in the DNA of the *Hox* genes which pattern the anterior-posterior (A-P) axis corresponds to the order in which they are expressed along the A-P axis. In other words, genes at one end of the chromosome are expressed at the head end of an embryo while genes at the other end are expressed toward the tail end.⁶ Although the pattern is not universally conserved as was once believed,⁷ nonetheless the conservation of this extraordinary homolog over hundreds of millions of years in many diverse lineages is still astonishing. As Rudolf Raff commented: “The conservation of a set of clustered genes over half a billion years is difficult to accept, but collinearity with body axis defies credibility. Yet it's true.”⁸

A wonderful piece of evidence of the extraordinary ubiquity and conservation of the toolkit genes, gene circuits, and developmental modules is provided by a remarkable experiment described in *Your Inner Fish*, by Neil Shubin.⁹ In this experiment, one particular toolkit gene product (the sonic hedgehog protein) has the same transforming effect on the development of the elements of shark fins as on mammalian and chicken

digits, causing a mirror-image duplication and change in the morphology of the fin elements depending on their distance from the source of sonic hedgehog protein. Shubin waxed lyrical about this remarkable result:

It means that this great evolutionary transformation [the transition from fish fins into limbs] did not involve the origin of new DNA: much of the shift likely involved using ancient genes, such as those involved in shark fin development, in new ways to make limbs with fingers and toes.

But there is a deeper beauty to these experiments on limbs and fins. Tabin's lab used work in *flies* to find a gene in *chickens* that tells us about *human* birth defects. Randy used the Tabin lab discovery to tell us something about our connections to *skates*. An "inner fly" helped find an "inner chicken," which ultimately helped Randy find an "inner skate." The connections among living creatures run deep.¹⁰

The deep homologies underlying limbs and fins were revealed in a recent study of a Turing-type mechanism responsible for digit patterning in mice. The authors comment:

The periodic pattern of skeletal elements evident in fins and mutant [mice] limbs strongly suggests that a self-organizing Turing-type mechanism of chondrogenesis is deeply conserved in vertebrate phylogeny. Our results further indicate that distal *Hox* gene dose regulates the number and spacing of skeletal elements formed, implicating distal *Hox* gene regulatory networks as critical drivers of the evolution of the pentadactyl limb.¹¹

Further evidence of the conserved genetic and developmental commonalities is illustrated by atavisms (i.e., "throwbacks" to an ancestral condition) such as the remarkable case of "chicken with teeth"¹² and the even more remarkable recently genetically engineered chicken with what the authors claimed was a "dinosaur snout."¹³

While not a member of the conserved developmental genetic toolkit, a fascinating mechanism which is utilized universally in generating biological patterns consisting of many repeated structures, is the *reaction-diffusion mechanism* first proposed by Alan Turing.¹⁴ Turing's idea was summarized by Cheng Chang as follows:

The model postulates that two chemicals, reacting and diffusing on some domain, may form spatially heterogeneous patterns of chemical concentration provided certain constraints are satisfied. Subsequent cell differentiation is assumed to take place according to local chemical concentration levels, with discrete cell fates assumed to have arisen via exposure to differing thresholds. Turing's reaction-diffusion model has been suggested as a mechanism for many types of biological patterning, including fish pigmentation... feather bud, scale and hair follicle formation... amongst others.¹⁵

It is worth noting in passing that the existence of genes, gene circuits, and developmental modules highly conserved in very distantly related organisms was entirely unexpected and unpredicted by defenders of the Darwinian faith. Based on the Darwinian conception that living things are highly pliable adaptive assemblages of parts, molded day-by-day in any direction at the hands of natural selection in the face of ever-changing contingencies, it was widely assumed by the pan-adaptationist makers of the mid-

twentieth-century neo-Darwinian synthesis that over the hundreds of millions of years that have elapsed since the last common ancestor of the animal phyla, every gene would have been crafted and re-crafted multiple times, including those involved in the assembly of the homologs, so that all evidence of any commonalities would have been lost millennia ago. Based on this widely held Darwinian expectation, Ernst Mayr, one of the giants of twentieth century evolutionary biology and himself one of the key makers of the mid-century synthesis, famously claimed that “the search for homologous genes is quite futile except in closely related species.”¹⁶ *There is hardly a prediction in science that has proved so woefully wrong!*

The following sections do not attempt anything remotely like a systematic review of this fascinating new field. My aim is primarily to focus on a few key findings and implications relevant to the major themes of this book, i.e., those which I think challenge Darwinism and support the alternative structuralist perception of nature.

5.1 Descent with Modification

There is no doubt that evo-devo has demonstrated that the evolutionary origin of the taxa-defining novelties, whether adaptive (e.g., feathers), or apparently non-adaptive (e.g., the pentadactyl limb and probably many other *Bauplans*), has involved the reorganization and co-option of existing gene circuits and the reutilization of universal developmental mechanisms. The landmark elucidation in Sean Carroll’s lab of some of the new gene circuits involved in the origin of the eye spots in Nymphalid butterfly wings is a classic example.¹⁷ This involved the co-option of the ancient *Distal-less* gene (a transcriptional factor), which is switched on in all bilateral animals where an appendage—wing, limb, antenna, etc.—extends or “sprouts” from the body wall. Carroll showed *Distal-less* is uniquely switched on in a set of cells in the wing which form the center of the eye spots. (Of course, there is more to eye spots than the expression of *Distal-less* in the center of the eye spot. The details of eye spot ontogeny are *very complex* and still not fully understood and several different evolutionary scenarios are on offer to account for their origin.¹⁸)

The discovery of the universal “toolkit” consisting of very widely conserved genes (like *Distal-less*) and developmental pathways is seen by most evo-devo researchers to provide new, powerful support for the concept of common descent. Carroll argues this point forcibly in Chapter 11 of *Endless Forms*.

But common descent, or “descent with modification,” has never been in doubt since Alfred R. Wallace’s famous “Sarawak Law Paper” (written in Borneo in February 1855), in which he concluded: “Every species has come into existence coincident both in space and time with a pre-existing closely allied species.”¹⁹ Given the facts that Alfred Wallace assembles in his Sarawak Law paper, descent with modification can hardly be doubted. Many instances of the coincidence could be cited. For example, the fish that most closely resemble the first amphibians lived in the same geographical region and at the same time (the late Devonian), which is highly suggestive of an ancestor-descendant relationship.²⁰

5.2 Elusive Causation

While the fact that the same toolkit is used universally to make eye spots, fins and limbs, etc., supports descent with modification, *it tells us very little about how the actualization of the homologs came about during the course of evolution.* The mere fact that the same

atoms are combined to make a brain or a paramecium, or that different cell types are combined to make different organs, or that the same twenty amino acids are combined in different ways to make the myriads of different proteins tells us nothing about how the different combinations were actualized.

And it certainly does not follow that, because organ A (an ancestral structure) arises out of a combination of a, b, c, d elements and novelty B (the descendant structure) arises out of another different combination of the same elements, that A was converted to B via a long series of tiny adaptive steps (i.e., a Darwinian functional continuum). The fact that the same atoms, proteins, cell types, gene circuits, gradients, or Turing mechanisms are utilized to make fins and hands, reptile scales and feathers, or fir cones and flowers provides in itself no evidence that the origin of such novelties occurred incrementally rather than by saltation. Nor does it imply that the transition occurred via a series of functional forms, or invalidate in any sense the claim defended here that the homologs represent inbuilt natural forms. Describing the genetic changes associated with the transition from A to B is not the same as explaining *how* B was derived from A.

The evo-devo description of the underlying gene circuits—master gene switches, genetic cascades, morphogen gradients, etc.—which conspire together in the making of evolutionary novelties is very impressive, but it is basically a *description*. And it is only a description of some, and probably only a tiny fraction, of the complex developmental mechanisms that were actually involved in the origin of the taxa-defining novelties discussed in the previous two chapters..

The widespread impression promoted by the Darwin propaganda machine that the evo-devo description of genetic changes somehow provides a causal explanation (and specifically a Darwinian one) of how the homologs came about is thus highly erroneous. So is the more general notion that evo-devo has solved “the problem of evolution” in favor of Darwin.

Lewis Held’s recent book *How the Snake Lost Its Legs* (2014) describes the underlying developmental and genetic changes that accompanied the origin of well over fifty different novelties.²¹ Held labels his chapters and sections with titles such as “How the butterfly got its spots,” “How the snake lost its legs,” “How the angelfish got its stripes,” “Why the chordate flipped upside down,” “How insects lost their hindlegs,” “How the horse got its hooves,” “Why the centipede has odd segments,” and so forth. The impression these titles convey (although I am not sure that this was intentional) is that the newly discovered inventory of genetic changes that accompanied these innovations provides a causal explanation of *how* the novelties arose and *how* evolutionary gaps were closed.

But this conflates an inventory of the genetic changes involved in the actualization of a novelty (which in every case is very incomplete) with a causal account. As Massimo Pigliucci cautions, descriptions of newly co-opted gene circuits and master switches, no matter how intricate, are not enough. As far as “how... major body plans evolved, or how evolution produced phenotypic novelties, a molecular study of master switches (which is most of what evo-devo has quickly become) can provide us with only a (very) partial answer.”²²

Evo-devo has certainly provided us with a new level of description of the changes involved in the origin of novelties that complements the pre-existing morphological description. Nevertheless, we knew long before evo-devo that there are large morphological differences between a fin and a limb, between a scale and a feather, between a hand and a bat's wing, and so forth. It was only to be expected that when the gene expression patterns underlying the actualization of the homologs were elucidated that there would be corresponding significant differences at the developmental genetic level as well.

The evo-devo revolution is still very much a work in progress and the genetic description itself is very far from complete. The challenge of attempting to elucidate the causal factors involved in the actualization of the homologs is complicated not only by the fact that there are many *genetic* changes still to be documented, but also by the fact that the ontogeny of every organ or complex morphological structure, including the homologs, involves, in addition to genomic changes, all manner of complex *epigenetic* changes.

The homologs described in the previous two chapters are higher-order phenotypic structures and their ontogeny inevitably involves far more than the mere expression of genes. The assembly of the gene products into the final phenotypic form of any organ or structure involves the activities of a complex integrated set of self-organizing emergent processes, which are in every case invisible from the perspective of genes.²³ Lewis Held acknowledges this himself: "Emergence... is ubiquitous in embryos... It endows their organs with a seemingly magical aura of spontaneity... Order and organization seem to come from nowhere, one shape changes seamlessly into another, and organs take on a life of their own."²⁴ As Andreas Wagner commented recently: "Known macroscopic innovations [accompanying the origin of an evolutionary novelty] are so complex that we do not understand all the required changes for any one of them."²⁵

The epigenetic factors involved in development are still largely mysterious, and it is going to be several decades before we have any real feel for the true complexity involved in the origin of any evolutionary novelty or anything like a full inventory of the causal factors involved. This is another reason why a mere inventory of genetic changes involved in the origin of a new homolog provides no real measure of the actual distance between the homolog and any hypothetical antecedent structure.

In this context, it is worth considering the necessity for very tight control of organ size during development—for example, to ensure that a human hand is seven centimeters across while a fly wing is only a few millimeters. The successful actualization of a new homolog would clearly necessitate tight control of organ size. Although some of the feedback systems have been identified, how these systems are integrated together to regulate organ size is almost completely mysterious. Recent papers convey something of the astonishing integrative complexity of the various processes involved.²⁶ For example, it has been established that organs "know" what size they "should be" and stop growing when they reach the target size based on clues arising from viscoelastic and other mechanical properties, i.e., higher order emergent properties of cells and tissues.

Amazingly, in many cases the process is largely autonomous and does not depend on external clues. For example, *Drosophila* imaginal wing discs, when cultured in an adult host, still grow to their appropriate target size. Remarkably, when the growth of the disc

slows in one developmental compartment, reducing the cell number and the size of that particular compartment, the cells “sense” the reduction and grow larger to ensure that the proper size of the compartment is maintained.²⁷ Something of the epigenetic complexity involved in the regulation of organ size is conveyed by this quote from a recent paper:

Growth of the wing disc [in *Drosophila*] is influenced by signals on multiple length scales... cell to cell, compartment-wide, disc-wide, and humoral (hormonal). Recent theoretical and experimental work... suggests that disc-wide coordination may be mediated, at least in part, by mechanical feedback (the length scale of which can be very long, depending on the viscoelastic properties of the tissue). The influence of mechanical effects (tension, compression) on cell growth is well established... such mechanical effects create an opportunity for disc-wide integral feedback control.²⁸ [all internal references removed]

Not only must an organ (*every* organ in *every* species) “know” its final adult size; it must know its appropriate size at all stages of development or controlled ontogeny would be simply impossible. A newborn baby’s finger is *necessarily* only a fraction of the size of an adult’s.

5.3 Internal Constraints

Despite the fact that there is still much to learn about the evo-devo changes associated with the origin of the homologs, one finding which is now well-established is the totally unexpected revelation (unexpected from Darwinian first principles) that what are referred to by evo-devo researchers as “constraints,” or what might also be termed “internal causal factors,” have played a far more important role in the origin of many of the homologs and *Bauplans* than was previously envisaged. Before evo-devo it was widely thought that internal factors played little or no role in shaping the course of evolution. But what is now increasingly obvious, as shown below by consideration of the origin of four major evolutionary innovations, is that internal causal factors have played a far more prominent role in the actualization of evolutionary innovations than cumulative selection.

a. Flipping Over

One of the most fundamental of all evolutionary innovations occurred when some ancestral chordate switched its body plan from the design previously shared by all other animal groups (in which the nerve chord is in a ventral position and the heart and main blood vessel are placed dor-sally) to a design which was the exact reverse (in which the nerve chord is placed dorsally and the heart placed ventrally), and which has remained invariant in all chordates ever since. The evidence for this dorsal-ventral inversion (D-V) was revealed when evo-devo studies showed that the signaling molecules that specify the back of an insect also specify the ventral side (the belly) of a vertebrate.²⁹ Before evo-devo had revealed that the same genes were involved in specifying the dorsal-ventral axis of chordates and non-chordates, no one took seriously Geoffroy’s suggestion, made early in the nineteenth century, that all animals shared the same basic body plan.³⁰

Self-evidently, Darwinian scenarios must confront the obvious question as to whether this transition was gradual or sudden. On the one hand, it is very hard to imagine how *gradual cumulative selection* could carry out such a radical re-engineering of the basic body plan. What mystifying adaptive path can be proposed along which the gradual

transition might have occurred? On the other hand, if the change occurred suddenly in one massive macro-mutational saltation, then Darwinian causation is ruled out of court altogether (see Chapter [11](#)).

Whatever the mode of the transition—gradual or sudden—common sense dictates that the actualization of such a drastic innovation would only be feasible if the organism in which the change occurred was in some sense *pre-adapted* for the change—that the “jump” to the current chordate body plan was already pre-figured into the internal design of our distant chordate ancestor. Even if there was an adaptive path, it would seem that this could only have been followed if it was compatible with the pre-existing developmental logic. Internal causal factors or constraints must be presumed to have played a major role, relegating whatever role cumulative selection might have played to that of a relatively insignificant bystander.

In the case of this dramatic innovation, the revelations of evo-devo provide no support at all for the Darwinian notion that cumulative selection is the major causal engine of evolutionary transitions.

b. The Insect Limb

Consider next the evo-devo discoveries regarding the gene circuits and developmental processes involved in the generation of the insect limb.^{[31](#)} As we saw in Chapter [3](#), underlying the vast adaptive diversity of all insect limbs is a *Bauplan* that is essentially invariant in all insect species.

The developmental module of the limb has been studied in detail in the fruit fly *Drosophila*, and its complexity is beyond belief. Evo-devo studies have revealed that the five segments of the limb are derived from five concentric regions of the limb imaginal disc. These concentric regions are specified by a concentration gradient of a morphogen, which diffuses from the center of the disc to the circumference. The inner ring develops into the most distal element of the limb—the tarsus—and the outer ring into the most proximal—the coxa. During metamorphosis, the disc becomes a cone and then a cylinder, which projects outwards with the center of the cylinder becoming the tip of the limb, the tarsus, and the outer rim becoming the most proximal segment, the coxa. Several other morphogen gradients are involved in addition to the radial gradient. Amazingly, one of the gradients is arc-shaped and curves around the circular disc, providing positional information that determines the position of eight bristle rows, each separated by an angle of forty-five degrees. The cells know their position on the circumference of the imaginal disc by sensing the concentration of the morphogen diffusing along the arc-shaped gradients.^{[32](#)} Marvelous though it is, this detailed description of this developmental module is not a causal explanation of *how* the module first arose.

One thing is clear: An incremental functionalist explanation for the origin of this developmental module is fantastically hard to imagine. Can one really believe that a succession of small adaptive steps led to the gradual putting together of the arc-shaped gradients? How did their emergence enhance step by step the reproductive fitness in a hypothetical insect ancestor? Again, what would be the adaptive advantage of eight rows of bristles separated by angles of forty-five degrees for a particular insect species? Why not six rows of bristles separated by sixty degrees? And what is the adaptive advantage of

five segments in the limb? What environmental contingency could the number five have served?

Knowing that a common limb-patterning network is used throughout the arthropods, utilizing many of the same toolkit genes as in insects,³³ and appealing to ancestry as Darwin did, tells us nothing of the ultimate causal factors involved or how the patterning mechanism came about. Moreover, despite many conserved commonalities and the fact that all insect legs conform to the same final “five segmental pattern,” there are also very significant differences in the way different groups of insects arrive at this common pattern, complicating further adaptive scenarios.³⁴

Trying to envisage the actualization of this complex patterning of the insect limb via long series of adaptive intermediates, each serving some functional necessity, (i.e., in purely Darwinian terms), leads again to Bateson’s “endless absurdities.” Again, common sense dictates that whatever role selection might have played in the becoming of the insect limb, the revelations of evo-devo in this instance, as in the case of the chordate D-V inversion, provide very strong support for the structuralist notion that *internal causal factors played an important if not decisive role in the actualization of this amazingly complex developmental module.*

c. The Insect Wing

What applies to the limb *Bauplan* and the D-V inversion applies equally to the tax-defining developmental module that generates the basic form of the insect wing, including the highly conserved *Bauplan* underlying the pattern of insect wing venation. The complexity of the development of the wing again is beyond belief and is perhaps even greater complex than in the development of the limb.³⁵ Every detail of the developmental program is an enigma in terms of adaptive gradualism. Part of the laying down of the basic plan of the wing in *Drosophila* involves the setting up of two orthogonal morphogen gradients which serve as the x and y axis in a planar Cartesian coordinate system which the cells of the imaginal disc can “read” to work out their position on the grid. The fate of each cell is determined by its precise position on the grid.³⁶ As Held remarks, it seems as if “flies discovered Cartesian coordinates long before René Descartes.”³⁷ This Cartesian grid plays a critical role instructing specific cells in specific regions of the disc to commence assembling the scaffolding of the wing, including the characteristic wing venation pattern. What succession of functional necessities could have gradually put together the two orthogonal gradients to set up the coordinate system in the ancestral insect is fantastically hard to imagine. Again it seems that internal, pre-existing causal factors must have played a predominant role in the actualization of this unique homolog, relegating selection to satisfy external conditions to a very peripheral role.

d. Centipede Segments

Consider a fourth *Bauplan*, the odd number of body segments in all centipede species. It was always a challenge for pan-adaptationism to envisage what mysterious selective advantage could have restricted centipedes to odd numbers of segments.³⁸ This long-standing puzzle has recently been solved, revealing yet again that another unique homolog is the result of internal developmental constraints.³⁹ The reason trunk segments are always odd is that in centipedes all additional segments added to the first seven segments—

comprising six segments making up the head and one segment (number seven) bearing the poison claw—are added as pairs because of a unique mechanism of segment generation *only found in centipedes*. Because the centipede adds segments two by two to the first seven segments, an odd number, the total number will always be odd. Although the actual causal mechanisms which initially led some ancestral centipede to adopt this particular unique developmental module are still obscure, it is very clear that it came about because of internal constraints unique to the biology of some ancestral centipede and *not because odd numbers of segments provided some selective advantage*. The evolution of the centipede head poses further problems in itself. Centipedes, insects, and crustaceans all have a head composed of six distinct segments and share a common developmental *Bauplan*.⁴⁰ Just what causal factors led to the initial incorporation of the six segments into the ancestral arthropod head and thereafter fixed the *Bauplan* over hundreds of millions of years in such a fantastically diverse group of organisms from millipedes to lobsters is of course unknown, but it is again hard to believe that adaptation was the only or major mechanism involved.

In these four representative taxa-defining homologs, it is self-evident that the emerging evo-devo picture provides no support whatsoever for the Darwinian claim that novelties came about during the course of evolution to serve a succession of functional ends. In these four cases, the structuralist inference that internal constraints and not cumulative selection played the key role in their actualization is difficult to refuse.

These four examples are not atypical. Evo-devo advances have revealed that in many, if not the great majority, of innovations in the history of life, *internal causal factors have played a predominant role*. Against all traditional expectations, Darwinian selection to serve adaptive ends could only have played, in most cases, a relatively peripheral causal role. Before evo-devo, no one would have imagined that a vast amount of organic order arises from internal constraints and causal factors within organisms themselves and is not imposed by selection. What was heresy only three decades ago is now accepted doctrine.

5.4 The Constraints Paradigm

The evo-devo revolution and the revelation that underlying the development of all organisms is a set of highly conserved gene circuits and integrated developmental modules that guide and constrain phylogeny without regard for the immediate adaptive needs of species, not only poses a widely acknowledged challenge (and indeed self-evident challenge) to pan-adaptationism but has also undermined completely the previous neo-Darwinian mechanistic view of organisms as analogous to contingent assemblages of LEGO blocks. According to this model, organisms are infinitely plastic “additive functional assemblages” which can be changed—LEGO block by LEGO block—from one shape to any other conceivable novel shape, bit by bit, without any significant constraints. On the contrary, all the evo-devo evidence suggests that there are deep and profound developmental constraints that work against such infinite pliability.

The new conception of organisms arising from the discoveries of evo-devo might be termed the “Transformer” model. Just as in a child’s Transformer toy action figure, the number of forms that can be reached by combining the basic parts in different ways is severely limited by the shape and properties of the component building bricks. The finite set of forms that can be assembled is pre-figured into the basic properties of the

constructional units. One might view the constraints imposed by the building units in a Transformer set (unlike LEGO bricks) as being analogous to those imposed in living things by the highly conserved tool-kit components and developmental modules.

Consequently, pigs will never fly—not only because of functional constraints (far too heavy!), but because of deep internal structural constraints in the way a pig is put together, which greatly restrict the available paths that adaptive evolution can take. On this view, the major novelties actualized during evolution could only have occurred if they were compatible with the pre-existing inner “developmental logic” of the organism, analogous to prefiguring of the Transformer components for a specific set of forms.

In other words, development rules! Or, more precisely, what rules is the collective constraints of toolkit elements, developmental pathways and modules that underlie the ontogeny of every class of metazoan organisms.

Intriguingly, Gould and Lewontin, with considerable prescience, wrote the following in their celebrated “Spandrels” paper: “If development occurs in integrated packages and cannot be pulled apart piece by piece in evolution, then the adaptational programme cannot explain the alteration of developmental programmes underlying nearly all changes of *Bauplan*.”⁴¹

The new evo-devo picture strongly implies that because the paths of evolution are highly constrained and because “development rules,” to jump into a new region of morphospace will necessitate escaping from the existing constraints. This might necessitate radical re-engineering of ontogeny. And this may mean that many major innovations cannot have resulted from the accumulation of everyday small “standing variations.”⁴² Major innovations may require major developmental shifts of a decidedly saltational nature.

Although there are some dissenters,⁴³ the existence of highly conserved developmental genetic mechanisms, gene circuits, and so forth restricting the paths of evolution has led to the widespread adoption of what might be termed a new *constraints paradigm* among many evo-devo researchers, who acknowledge that the deep logic of development is bound to restrict the direction of variation and hence evolutionary change along limited paths.⁴⁴ But what is really radical about the “constraints paradigm” is that the constraints restrict the paths of evolution *without any regard for immediate adaptive function*.⁴⁵ The notion of deeply shared non-adaptive internal causal factors channeling the paths of evolution without regard to immediate adaptive needs is certainly heretical, and it is small wonder that, as Müller and Pigliucci concede, many leading biologists feel that evo-devo presents “challenges to the received theory... so substantial that no reconciliation with the classical framework [Darwinian, incremental functionalism] is at all possible.”⁴⁶

Echoing the same sentiment, Lindsay Craig argued that “The foundation of the Modern Synthesis framework, theoretical population genetics [the basis of classical neo-Darwinism], faces significant, perhaps insurmountable challenges from the concepts highlighted by EvoDevo.”⁴⁷ Wallace Arthur, a leader in the field, likewise acknowledges that “Many scientists working in evo-devo today, whether in its molecular, organismic, or paleontological ‘wings,’ believe that novelties and body plans do require some *special*

explanation” beyond incremental functionalism.⁴⁸ And as noted in Chapter 1, Fodor and Piattelli-Palmarini concur.⁴⁹

In effect, the evo-devo revolution has changed the conception of the organism as infinitely malleable in the hands of the natural selection to one in which this malleability is highly constrained by internal causal factors. The change is a landmark in the history of biology because the notion that internal causal factors have constrained the paths of evolution is exactly what structuralism implies and represents a definite step away from classic Darwinism. Indeed, it can be seen as a first step by mainstream biology back towards a structuralist perception of the natural order. These internal constraining factors are precisely the sorts of agents that must be postulated if descent with modification proceeded, as structuralism implies, “nomogeneously” and if a limited set of Types and the paths to their actualization are built into nature.

So both the structuralist and evo-devo paradigms converge in the postulate that internal causal constraints have played a major directing role in the evolution of life. Of course, most evo-devo workers do not view the internal factors (the toolkit and the associated developmental genetic constraints) which channel life along restricted paths as arising, as “strong” structuralists have always maintained, from emergent physical properties of organic systems, but from *previous (ancestral) rounds of adaptive evolution*: constraints imposed by history, and not by nature.⁵⁰

It is not possible at this juncture to make any final judgment as to the ontological status of the components of the toolkit, whether they are ultimately the product of natural lawful processes (like atoms or crystals) as I believe, or contingent elements as mainstream biology asserts. Nevertheless, the possibility exists that the toolkit components—*Pax6*, the collinearity of the genomic arrangement of the Hox genes with A-P body axis, widely shared gene regulatory networks, developmental modules and so forth⁵¹—are lawful natural forms which arose as a result of internal causal factors operative in the ancestral primeval organisms from which all multicellular animals descended. Their astonishing invariance may hint at their fundamentally robust natural status. If true, this would mean that the constraints and internal factors are parts of the natural order, and the evolutionary paths they have facilitated were built into nature from the beginning, precisely as structuralism implies. And it would mean that the advent of evo-devo is not just a first tentative step towards structuralism, but rather a massive historical step back in that direction.

5.5 Summary

The fact that the same toolkit components were co-opted to actualize the novel tax-defining homologs may support descent with modification, but in itself provides not the slightest justification for assuming that they were acquired piecemeal, bit by bit, in successive adaptive steps as classic Darwinism asserts.

Moreover, in specific cases where the developmental mechanisms and genes involved in the ontogenesis of the homolog are known in considerable detail (such as the insect limb and wing), the evidence suggests, in conformity with structuralist predictions, that internal causal factors have played a major if not decisive role in their actualization, whatever additional role selection may have played.

As far as the constraints paradigm is concerned, whether one views conserved gene and gene circuits as ancient adaptations, as most evo-devo researchers do, or whether one views them as primarily non-adaptive, arising ultimately from the intrinsic properties of living matter, as structuralism predicts, the implication is clear: The paths of evolution and the actualization of novelties were determined to a considerable extent by what are clearly “internal factors.” And this means Darwinian selection is not the only or even the main factor that determined the shape and main branches of the great tree of life.

Overall, the developing picture is certainly consistent with the typo-logical notion that the tree of life and the taxa which form its branches are, as Owen and nineteenth-century biology believed, pre-ordained into the order of things, part of the fine-tuning of the cosmos for life as manifest on Earth.

6. The Tree of Life and Distinctive Types

As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great tree of life, which fills with its dead and broken branches the crust of the earth.

Charles Darwin, *On the Origin of Species* (1872), Chapter 4.

6.1 The Types and the Tree of Life

In *Evolution: A Theory in Crisis*, I wrote:

The hierarchic patterns of class relationships are suggestive of some kind of *theory of descent*. But... [they do not] tell us anything about *how* the descent or evolution might have occurred, as to whether the process was gradual or sudden, or as to whether the causal mechanism was Darwinian, Lamarckian, vitalistic or even creationist. Such a theory of descent is therefore devoid of any significant meaning and equally compatible with almost any philosophy of nature....¹

The same hierarchic pattern which may be explained in terms of a theory of common descent, also, by its very nature, implies the existence of deep divisions in the order of nature.²

It is a major fallacy to think that belief in distinct Types as immanent features of nature and the notion of descent with modification are incompatible. On the contrary, just so long as Types are defined by unique novelties (homologs or synapomorphies), which are *themselves not approached gradually via transitional forms*, then the Types themselves can be said to be absolutely distinct and can arise suddenly at that moment in phylogeny when members of any lineage acquire a novel homolog.

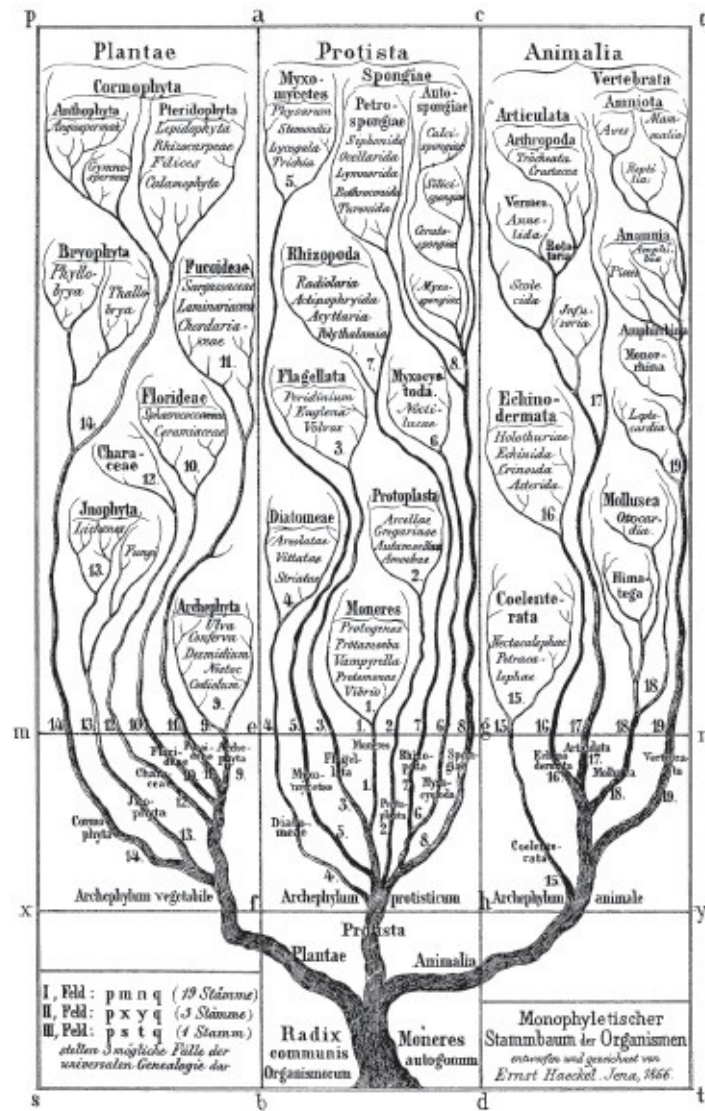


Figure 6-1. Tree of Life. From *Generelle Morphologie der Organismen* (1866) by Ernst Haeckel.

Consider the origin of the Tetrapoda. This happened when some members of the lobe-finned fish tribe acquired limbs—a dramatic novelty which opened up the possibility of terrestrial life and led eventually to the colonization of the land by vertebrates. If this novelty was acquired quickly or *per saltum* (by a leap or bound without intervening stages), then no intermediates leading to Tetrapoda will ever be found, because they never existed! One can say properly that the new clade Tetrapoda, defined by its novel primal pattern—the limb—was not led up via transitional forms. But this does not mean that the first tetrapods did not descend or arise from lobe-finned fish.

Typology is perfectly consonant therefore with descent with modification. Each cladogram is witness to descent with *modification* and the existence of distinct Types. The *modifications* are novel taxa-defining homologs, acquired during the process of descent along a phylogenetic lineage, each of which defines a new Type. In the case of the Tetrapoda, there is a natural ancestor–descendant relationship (e.g., between lobe-finned fish and early amphibians), but because the descendants (amphibians) have acquired the new Type-defining novelty (the limb) that their immediate ancestors (lobe-finned fish) lacked, they consequently belong to a newly emergent Type, Tetrapoda.

The term “descent with modification” describes this process of change through time far more precisely than the term “evolution,” because the term “evolution” implies the

gradual emergence of a new type via a long series of transitional forms—a notion I strongly reject and for which, as we have seen in the previous three chapters, there is simply no empirical evidence. Descent with modification implies a pattern of descent through time, where extant forms have descended with modification from common ancestral forms, right back to the last common ancestor of all extant life. But the fact of descent with modification cannot be taken as evidence for Darwinian causation or as support for any sort of gradualism. *Evidence for descent with modification is not evidence for adaptive continuums of transitional forms.* Just so long as each newly acquired defining homology is not led up to by an evolutionary sequence, all talk of “transitional forms” or “intermediate forms” and even the use of the word “evolution” is largely empty rhetoric. To talk of transitional forms between, say, amphibians and fish, when one of the defining homologies of amphibians is the tetrapod limb—which, as we shall see in Chapter 9, is not led up to by a long series of adaptive transitional forms—is sophistry!

Of course, on the theory of descent with modification, some fish must have been ancestral to the first tetrapod. There are many similarities between lobe-finned fish and the first amphibians, and both tetra-pods and lobe-finned fishes can be included in the same clade. We *can* say that descent with modification did occur; whether we can say that amphibians “evolved from fish” is altogether a different matter, especially if the term “evolution” carries, as it almost universally does, the connotation of gradualism and the additional connotation of Darwinian adaptive gradualism.

One of the greatest ironies in the field of evolutionary biology is the point made by Rupert Riedl (referred to in Chapter 3) that if the homologs were not in fact distinct, if no Type-defining homologs existed, then it would be impossible to build a tree of life showing the derivation of all extant forms of a particular clade from a common ancestor.³ It is easy to see that this must be so. Imagine a counterfactual world in which the homologs are not fixed. Suppose that in such a counterfactual world, that after the origin of the one, two, five pattern of the tetrapod limb, in one hypothetical “tetrapod lineage” the pattern (being variable) changed to one, one, six then later to two, two, four. And in another lineage, the pattern changes to one, three, six, and then one, one, two. In yet another lineage, the pattern remains the same. In such a resultant chaos of patterns it might be impossible to identify the ancestral pattern and infer descent with modification of all “tetrapods” from a common ancestor from the study of extant forms.

Or imagine an even more extreme counterfactual world in which lineages regularly lost all their Type-defining homologs. In such a hypothetical universe, classification would pose intractable problems and ancestor-descendant sequences would be impossible to identify. It is surely the “best kept of all evolutionary secrets,” that the inference to descent with modification depends on the fixity of the Type—or, more properly, the invariance of the taxa-defining homologs. Typology implies descent with modification, and evolutionary biologists are only able to argue for descent with modification precisely because the *homologs do not generally undergo any change after their first actualization*—because typology holds! How ironic that for Richard Dawkins and other defenders of the Darwinian faith the very notion of *evolution* depends on the fixity of the Type.

6.2 Coyne versus Gould

Despite the evidence, many evolutionary biologists make statements that appear to

directly contradict the claim that the Types are real and defined by unique taxa-defining novelties, by alluding to “transitional forms” leading from one Type to another. Jerry Coyne, for example, claims:

We have many examples of transitional fossils *between* what anyone would consider different kinds: fish and amphibians (like *Tiktaalik*...), between amphibians and reptiles, between reptiles and mammals, between reptiles and birds, between land animals and whales, and of course, between early and modern humans, with early fossils showing intermediacy between the features of apelike ancestors and modern humans.⁴

Such claims seem to imply that there are no distinct Types or Type-defining novelties. Yet, as we have seen in Chapter 3, it is the view of many researchers that there are indeed unique Type-defining novelties and that accounting for their origin is one of the major tasks of evolutionary theory. This is what Gould, for example, says about transitional forms: “Can we invent a reasonable sequence of intermediate forms—that is, viable, functional organisms—between ancestors and descendants in major structural transitions?... I submit, although it may only reflect my lack of imagination, that the answer is no....”⁵ About one relatively simple novelty—rodent cheek pouches—Gould comments:

The... pocket gophers and... kangaroo rats and pocket mice... have invaginated their cheeks to form external fur-lined pouches with no connection to the mouth or pharynx. What good is an incipient groove or furrow on the outside? Did such hypothetical ancestors run about three-legged while holding a few scraps of food in an imperfect crease with their fourth leg? Charles A. Long has recently considered a suite of preadaptive possibilities (external grooves in burrowing animals to transport soil, for example) and rejected them all in favour of discontinuous transition. These tales, in the “just-so story” tradition of evolutionary natural history, do not prove anything. But the weight of these, and many similar cases, wore down my faith in gradualism long ago.⁶

In the same vein, Gould elsewhere comments, as mentioned in Chapter 1: “The extreme rarity of transitional forms in the fossil record persists as the trade secret of paleontology.”⁷

How can Coyne’s claim be reconciled with Gould and the many other researchers who do acknowledge the existence of Type-defining novelties? The explanation is that Coyne and Gould are referring to different things.

When Coyne talks of intermediates between fish and amphibians, he cannot be alluding to the origin of the tetrapod limb, which defines the Tetrapoda, and unambiguously separates fish (all fish) from amphibians, and is not led up to via transitional forms. If his intention is to claim this, then his claim is massively misleading. What he is claiming, I think, is that there are some fish—lobe-finned fish—that *are closer to amphibians* than the ancestral groups of fish from which they were derived and can be deemed intermediate in the loose sense that they possess certain characteristics possessed by amphibians but not by other fish.

Every cladogram illustrates transitional forms in this loose sense. For example, frogs

lack many of the defining traits of mammals, but do share limbs with the mammals, while no fish possesses this particular homolog. So you can argue, with Coyne, that frogs are in this loose sense intermediate or transitional between mammals and fish, and so forth. Again, you can claim that reptiles share with mammals the amniotic membrane, while no amphibian possesses this homolog. But as mammals also possess many unique traits not possessed by reptiles, you can loosely describe reptiles as being intermediate or transitional between amphibians and mammals. If descent with modification involves the acquisition along a lineage of a succession of novel homologs, this is bound to lead to organisms which possess a mixture of the “older” homologs of the ancestral clade from which they were derived and the new homologs which define the clade to which they belong. Such species are termed mosaics, possessing a mixture of new and old traits.

Coyne gives a good example in his *Why Evolution is True* of an ant, which combines older defining features (synapomorphies) of the Hymenoptera and newer taxa-defining novelties of the ants.⁸ Many other mosaics could be cited: *Archaeopteryx* (reptilian teeth, long tail, wings and flight feathers), Platypus (egg-laying, mammary glands, hair), *Australopithecus* (small ape brain, bipedal human stance).

Gould, however, is claiming along with other researchers (including Rupert Riedl, Gareth Nelson, Massimo Pigliucci, Günter Wagner, and other authors cited in Chapter 3) that the novelties *themselves are not led up to via transitional forms and are genuine novelties*.

Thus, there is no contradiction between the claims of Coyne and Gould. Under a typological viewpoint, there are “transitional forms” between man and fish, which in a loose sense form a linear evolutionary series of forms increasingly resembling a human being and sharing an increasing number of the taxa-defining novelties possessed by mammals. But there are *no transitional forms leading to the actualization of each novelty*. The successive appearance of novel homologs is the key series of events which generated the overall pattern of life on earth, a series which, in the words of Owen in the last paragraph of *On the Nature of Limbs*, guided life “from the first embodiment of the vertebrate idea under its old Ichthic vestment, until it became arrayed in the glorious garb of Human form.”

The other example of transitional forms widely cited as evidence for evolution are those many cases in the fossil record where there is an obvious incremental sequence of morphological changes in the successive members of a particular lineage. The classic case is the evolution of the horse, which evolved from a five-toed ancestral species *Eohippus* via three-toed intermediate proto-horses to the modern horse over a period of fifty million years.⁹ Many other similar evolutionary sequences exist and are depicted in standard texts of paleontology as evidence for evolution.¹⁰

Many of these sequences are not quite as linear as often made out. Nonetheless, they do show an evolutionary trend in a particular morphological feature. Thus, such trends support the notion of descent with modification; and because they often involve what are clearly adaptive changes, they may be construed to support Darwinian adaptive evolution—e.g., in the case of the horse, the changes may have facilitated more efficient running on drier land.¹¹

At the same time, when examined in detail, these “trends” either involve change to an adaptive mask and *not to an underlying homolog* or, in the case of *many* long-term trends, give no hint that they might have arisen to serve some environmental constraint, thus they provide a major challenge to Darwinism.¹²

Intriguingly, perhaps the most widely cited functional transformation alluded to as “evidence for evolution” is the functional transformation of three skeletal components of the upper and lower jaw in primitive fishes into the three ear ossicles—the malleus, incus, and stapes, respectively—in mammals.¹³ These skeletal components are Meckel’s cartilage, the palatoquadrate (formed from the ventral and dorsal parts of the first pharyngeal arch, the mandibular), and the hyomandibular bone from the dorsal part of the second pharyngeal arch (the hyoid), which played a role in bracing the two parts of the jaw together. In reptiles, these three skeletal components are called the quadrate (which articulates with the articular bone in the lower jaw); the articular bone in the lower jaw; and the stapes (which transmits sound from the outer to the inner ear in all tetrapods). So these three elements of the first and second pharyngeal arches were utilized firstly to form the jaws and a bracing hinge in primitive fishes; they were utilized secondly in reptiles to form the stapes in the middle ear and part of the lower jaw and the joint linking the lower jaw to the skull; and they were utilized thirdly in mammals to form the three bones in the middle ear.

But yet again, although these changes do support the notion of descent with modification, when these transformations are considered in depth, it is clear that a series of adaptive masks have been imposed on a changeless underlying *Bauplan*. As Riedl comments:

The extent to which these three units have retained their relationship over a period of 400 million years is striking, for it is in spite of all sorts of adaptive selection demonstrated by their complete change of function, structure and position. We can therefore raise the old question more specifically: what is this superimposed coherence which so steadfastly keeps them together?¹⁴

The co-option of the same three bones for very different purposes during vertebrate evolution¹⁵ illustrates descent with modification, but, ironically, it also provides one of the most stunning examples of invariance of an underlying *Bauplan*.

6.3 Caveat

In this context, I have a clarification to make regarding the title my earlier book *Evolution: A Theory in Crisis*. As that book was a critique of Darwinian causation and not of the theory of common descent, a more appropriate title might have been *Darwinism: A Theory in Crisis*. I think I used the words “evolution” and “Darwinism” too loosely, conveying the impression that they referred to the same thing, when of course these are two very different concepts. In many places, where I should have used the term “Darwinian evolution” rather than “evolution,” I created the impression that I doubted the notion of common descent.¹⁶ But many other authors are also guilty of the same confusion between “evolution” and “Darwinism” (meaning the Darwinian mechanism). Coyne, in a prominent critique of Michael Behe’s *Edge of Evolution*, continually cites evidence for evolution as evidence for Darwinism and against Behe.¹⁷ And at the *Kitzmiller v. Dover*

trial, Kenneth Miller conceded in one part of his testimony that the term “evolution” is sometimes used to describe descent with modification and at other times the mechanism of natural selection.¹⁸

6.4 Summary of the First Six Chapters: The Discontinuity of Nature

There is a tree of life. There is no doubt that all extant life forms are related and descended from a primeval ancestral form at the base of the tree. But there is no evidence to support the Darwinian claim that the tree is a functional continuum where it is possible to move from the base of the trunk to all the most peripheral branches in tiny incremental adaptive steps. On the contrary, all of the evidence as reviewed in these first six chapters implies that nature is clearly a *discontinuum*. The tree is a discontinuous system of distinct Types characterized by sudden and saltational transitions and sudden origins of taxa-defining novelties and homologs, exactly as I claimed in *Evolution* thirty years ago. The claim has weathered well!

The grand river of life that has flowed on earth over the past four billion years has clearly not meandered slowly and steadily across some flat and featureless landscape, but tumbled constantly through a rugged landscape over endless cataracts and rapids. No matter how unfashionable, no matter how at odds with current thinking in evolutionary biology, there is no empirical evidence for believing that organic nature is any less discontinuous than the inorganic realm. There is not the slightest reason for believing that the major homologs were achieved gradually via functional continuums. It is only the *a priori* demands of Darwinian causation that have imposed continuity on a basically discontinuous reality.

No matter how “unacceptable,” the notion that the organic world consists of a finite set of distinct Types, which have been successively actualized during the evolutionary history of life on earth, *satisfies the facts far better than its Darwinian rival*.

Firstly, the absence of transitional sequences leading from antecedent structures to the each of the thousands of Type-defining homologs actualized during phylogeny is far more consonant with typology than Darwinism. The Darwinian claim that all the homologs were gradually achieved over millions of generations by incremental functionalism—the genetic code, human language, the flower, the diaphragm etc.—is a phantasm. The near-universal absence of intermediates leading from antecedent structures to the homologs speaks volumes. Secondly, as we saw in Chapter 4, on any Darwinian account, one must assume that previously plastic forms, “the homologs in the making,” became fixed for some absolutely mysterious reason at specific points in phylogeny and thereafter remained invariant. This is a curiously non-adaptive specter, and highly incongruous in the context of a biology wedded to pan-adaptationism and a biological worldview which posits all living forms as part of an ever-mutating continuum. Thirdly, and perhaps most importantly, in the case of many of the homologous patterns—and particularly the *Bauplans* like the tetrapod limb—there is *no evidence* that they are basically adaptive forms. Certainly in the vast majority of cases, they have never been shown to serve some functional end. Self-evidently, in accounting for the evolutionary emergence of homologs that serve no specific adaptive function, structural explanations win hands down.

True, there are rare cases where a taxa-defining novelty has been lost. One example is the loss in all extant Cetacea of the typical mammalian pattern of dentition. In all extant toothed whales, all the teeth have the same simple peg-like design.¹⁹ Another example might be the loss in the cheetah of retractable claws, one of the defining traits of the cats, inferred from recent phylogenetic studies showing Felidae evolution, which imply that the cheetah must have evolved from ancestors with retractable claws,²⁰ although other sister clades of the cats in the more inclusive clade Feliformia also have retractable claws.²¹ Actually, the loss is quite minor. Cheetah claws are weakly retractile but lack protective skin folds and so are always visible and blunt compared with the claws of other cats.²²

Similarly, many species of cavefish have lost their eyes.²³ Snakes during their subterranean sojourn lost their foveas (the part of the retina devoted to high resolution vision), a basic visual trait of their lizard ancestors.²⁴ But these and other rare cases are the exceptions that prove the rule that taxa-defining homologs in the vast majority of cases remain invariant after their evolutionary emergence in all members of the clade they define.

I also acknowledge that some apparently non-adaptive Type-defining traits may eventually be explained in terms of Darwinian functionalism. As mentioned in Chapter 3, the dentition in all extant mammals (except for extant Cetacea and armadillos) is based on the same basic dental pattern: no more than forty-four teeth, and no more than three incisors; one canine; four pre-molars; three molars in each dental quadrant; and precise dental occlusion (the exact fitting of the projections of the cavities of the molars to allow efficient mastication of food). Gradual adaptation for more efficient mastication of food and the need for precise dental occlusion must have played a significant role in the evolution of at least some features of this pattern, and the differentiation of the teeth into different categories (heterodonty).²⁵

But as to the numeric pattern itself—the three, one, four, three constraint—there must have been underlying non-adaptive developmental constraints involved in imposing this specific numeric pattern early in mammalian evolution. Why not two, one, four, three? Although the premolars and molars perform different functions (the premolars hold and grind, the molars grind),²⁶ it is hard to see on purely adaptive grounds why the basal pattern of four pre-molars and three molars was preferred and fixed.

Finally, I would like to describe briefly and say something in defense of my own typological model.²⁷ As is obvious from the text of the previous three chapters, I see the Types (as did Owen and many pre-Darwinian typologists) as part of the order of nature, a manifestation of the universal fitness of nature for life, and the actualization of their defining homologs during the course of evolution to be the inevitable outcome of perfectly natural processes. They are no less natural—and no less inevitable—than other complex ends manifest in the natural world.

I view the Types as being in some sense analogous to the stable atoms of the periodic table. And I view their actualization in the course of phylogeny to have come about in many cases in a relatively saltational manner; thus, the organic realm can be considered like the periodic table of elements: a genuine natural discontinuum of stable material forms. Although I do believe that the origin of many of the homologs occurred by saltation (as this is where the evidence points), I have no fixed view of how saltational

were the jumps or whether in many cases their actualization, like the formation of stable atoms (such as lead) may have come about via unstable and elusive short-lived transitional forms (analogous to the radioisotopes of Uranium), which are currently empirically unknown and often theoretically hard to envisage. It is in this sense, viewing the jumps as analogous to those between stable atoms, that I am using the terms “discontinuous,” “discontinuum,” etc. throughout the book.

Structuralists have long viewed the origin of life and of the major Types in discontinuous or saltational terms. But it is important to point out that structuralism and the notion that organic forms are the product of natural processes do not necessitate saltation. Natural forms and processes may be glacially slow or spectacularly fast: A continent slides at one centimeter a year across the globe and a stalactite may take a million years to grow a few centimeters, while a supernova explodes in a fraction of a second.

While Darwinism demands absolute gradualism if selection is to be the agent of change, structuralism is perfectly compatible with either mode of origin. My own saltationalism is based not on any logical necessity of structuralism but on the empirical facts that the homologs are not led up to via transitional forms and that many, like Owens’s “primal patterns,” give every appearance of being abstract non-adaptive patterns.

Whatever the mode of transition, according to the strong version of structuralism I am defending here, the origin of these homologs was determined primarily by internal causal factors, ultimately derived from the basic properties of biomatter and not by the external action of natural selection via long series of functional intermediates as Darwinism implies. I do not deny a causal role for selection in some or perhaps many of the transitions, but I believe that its role was secondary to the primary internal and natural causal factors which drew life, to cite Owen, “nomogenously” from chemistry to its cellular stirrings in the primeval ocean to the diverse forms which grace the world today.

As to how the successive emergence of the taxa-defining homologs actually occurred as evolution unfolded, I take the view that all the various vertebrate homologs actualized during the course of evolution—limbs, amnion, hair, mammary glands, feathers—were in some sense prefigured into the design of the vertebrate Type, what one might call the *Urvertebrate*. However, in envisaging that the entire subsequent unfolding of vertebrate evolution from jawless fish to primates was in some sense prefigured in the *Urvertebrate*, I do not see this as a simple kind of preformism, i.e., that all the information for the actualization of the successive vertebrate taxa-defining homologs was already present in the *Urvertebrate* in the way gene-centrists claim all the information necessary for development is in the egg or in DNA sequences.

Rather, on the typological view I am inclined to favor, phylogeny is emergent and analogous to epigenesis in ontogeny. Just as all the various organs and structures of an organism emerge from the initial egg in a developmental process that is profoundly epigenetic—involving all manner of emergent self-organizing processes, which arise successively as embryogenesis proceeds—so I see the vertebrate homologs as arising in analogous fashion during the course of evolution.

In this model, the *Urvertebrate* may be thought of as a ball poised at the top of a

slope in a complex natural multidimensional landscape that contains a prefigured set of facilitated paths to the valley bottom. On this naturalistic view, phylogeny is strictly analogous to the folding of a protein into its native form where the amino acid sequence is drawn through a set of preferred structures to the emergent vastly complex 3-D arrangement of the atoms in the native form of the protein. In this model the evolutionary pathways are in nature, not in the *Urvertebrate* itself. The facilitated paths are part of nature's deep causal structure, prefigured into the order of things from the beginning, drawing the various vertebrate subtypes from the *Urvertebrate* during the course of evolution.

Typology has the merit of unifying all biological becoming within the same lawful framework. The folding of a protein, the ontogeny of an individual organism, and the grand march of phylogeny are all seen on this view to be analogous and inevitable emergent ends of nature's deep structure. Moreover, the same paradigm unifies both the inorganic and organic realm and makes intelligible the discovery of the extraordinary fine-tuning of the laws of nature and the structure of the cosmos for the carbon-based life forms that exist on earth. Typology holds out the immensely beautiful possibility of a completely scientific explanation of the phenomenon of life based on natural law rather than the vagaries of contingency, a goal which is surely at least worthy of respect. For it is, after all, the same end which all science and rationality has sought since the beginning of the scientific revolution.

In these first six chapters, I have presented my reasons for viewing the biological realm as a discontinuum of isolated Types and pointed out that many of the Type-defining homologs give no indication of being adaptive. I have argued that this empirical picture is incompatible with Darwinism but supportive of typology. Standing on their own, I think the evidence and arguments offered in these first six chapters are sufficient to make a very strong case for my thesis. In the rest of the book, I will provide further evidence for this view by considering in depth the origin of a number of specific novelties. Near the end in Chapter [13](#) I will also present additional positive evidence for typology.

7. Bridging Gaps: Cells and Proteins

On the theory of natural selection we can clearly understand the full meaning of that old canon in natural history, “*Natura non facit saltum*.” This canon, if we look only to the present inhabitants of the world, is not strictly correct; but if we include all those of past times... it must on this theory be strictly true.

Charles Darwin, *On the Origin of Species* (1872), Chapter 6.

Putting aside for the moment consideration of the ontological status of the taxa-defining novelties and the question, in the case of the *Bauplans*, as to whether these enigmatic patterns are abstract as Owen believed or adaptive as Darwin claimed, one thing is clear: Explaining their origin in terms of gradual cumulative selection poses, in most cases, insurmountable difficulties. And this is precisely what one would expect if these taxa-defining novelties represent real “gaps” or discontinuities in nature’s order.

In *Evolution: A Theory in Crisis*, I claimed that empirical discontinuities seem to coincide invariably with a major conceptual discontinuity in envisaging how they might have come about—a coincidence which strongly reinforces the notion that the gaps are real and not mere sampling errors.¹ I have no reason to retract that claim. On the contrary, thirty years on, I believe it is more secure than ever.

Just how hard it is to provide theoretical scenarios to bridge these gaps is obvious from the sorts of mental gymnastics necessary to explain how many of the novelties were acquired in terms of cumulative selection. Indeed, I would argue that in so many cases not even implausible just-so stories are on offer.

In Chapter 5, I considered briefly four taxa-defining novelties, including the developmental patterning of the insect limb and wing as occurs in *Drosophila*, and I showed that envisaging how they arose by cumulative selection raises severe problems. Over the next four chapters, I consider ten additional taxa-defining novelties: the most inclusive of all, the basic cell type characteristic of all life on earth (which raises the origin-of-life problem); the enucleation of the red cell; the endometrial stromal cell; protein-coding genes (the simplest and most basic of all evolutionary novelties); the angiosperm flower and double fertilization; the tetrapod limb; the feather; the wing of the bat; the life cycle of the eel; and human language and our higher mental faculties. As I show in every case, it is very difficult to envisage how these novelties might have come about via a series of small adaptive steps.

The chosen examples are, of course, just a tiny fraction of taxa-defining novelties that prove hard to account for in terms of cumulative selection. I could have included, had space allowed, a great many more classic examples, including the turtle body plan,² mammary glands,³ the diaphragm,⁴ hair, and others. Richard Goldschmidt, in his heretical *Material Basis of Evolution*, listed a great many more.⁵

There is admittedly an element of tedium in carefully considering several examples,

but for the sake of completing the argument, there is no alternative. To claim that the gaps can't be plausibly closed by Darwinian cumulative selection, yet not to back up this claim with relatively detailed consideration of at least a few cases, would be leaving the argument very much in the air. As always, the devil is in the details! To validate typology it is necessary to clearly establish that the "gaps" are real, i.e., that no conceivable adaptive continuums are known that can plausibly bridge the discontinuities and account for the origin of the taxa-defining novelties.

7.1 The Origin of the Cell

Consider the most inclusive of all ground plans in the biological realm, one that has not changed for 4,000 million years: the *Bauplan* or "ground plan" of the cell, the basic unit of all life on earth.

As with other taxa-defining novelties, there is no evidence that any fundamental changes have occurred in the basic design of the cell system since its origination. The cell membrane, the basic metabolic paths, the ribosome, the genetic code, etc., are essentially invariant in all life forms on earth. And absolutely no plausible well-developed hypothetical evolutionary sequence has ever been presented showing how the cell might have evolved via a series of simpler cell-like systems.

In *Evolution: A Theory in Crisis* I wrote: "Between a living cell and the most highly ordered non-biological system... there is a chasm as vast and absolute as it is possible to conceive."⁶ Thirty years on, the situation is entirely unchanged. Despite a vast increase in knowledge of supra-molecular chemistry and of cell and molecular biology; the unexpected discovery of ribozymes; and an enormous effort, both experimental and hypothetical, devoted to providing a gradualistic functionalist account of the origin of life in terms of a long series of less complex functional replicating systems (e.g., the much-touted "RNA world") leading from "chemistry" to the cell, no one has provided even the vaguest outlines of a feasible scenario, let alone a convincing one.⁷ A yawning gap still persists—empirical and theoretical.

a. The Clutter Problem

A major unsolved problem in the origin-of-life field is what Gerald Joyce referred to as the "clutter problem": the problem that prebiotic syntheses invariably generate very heterogeneous solutions of organic compounds. This makes it very difficult to imagine how ordered linear polymers, made of only the canonical monomers, amino acids, or nucleotides, could ever have been assembled.⁸ As Steven Benner commented:

Prebiotic chemistry could produce a wealth of biomolecules from nonliving precursors. But the wealth soon became overwhelming, with the "prebiotic soups" having the chemical complexity of asphalt (useful, perhaps, for paving roads but not particularly promising as a wellspring for life). Classical prebiotic chemistry not only failed to constrain the contents of the prebiotic soup, but also raised a new paradox: How would life (or any organized chemical process) emerge from such a mess?⁹

Joyce says this about the problem:

Ribose, phosphate, purines and pyrimidines all may have been available...

These may have combined to form nucleotides in very low yield, complicated by the presence of a much larger amount of various nucleotide analogues. The nucleotides (and their analogues) may even have joined to form polymers, with a combinatorial mixture of 2',5'-, 3',5'- and 5',5'-phosphodiester linkages, a variable number of phosphates between the sugars, D- and L- stereoisomers of the sugars, α - and β -monomers of the glycosidic bond, and assorted modifications of the sugars, phosphates and bases... It is difficult to visualize a mechanism for self-replication that... would be impartial to these compositional differences... The chief obstacle to understanding the origin of RNA-based life [but the same applies to protein–DNA based life] is identifying a plausible mechanism for overcoming the clutter problem wrought by prebiotic chemistry.¹⁰

b. Autocatalytic Sets or Template Replication

Assuming that the basic building blocks—sugars, amino acids, lipids and nucleotides—could have accumulated somewhere on the early earth, in Darwin's "warm little pond,"¹¹ and assuming that the clutter problem could be overcome, the question then arises: How were the polymers assembled into the first replicating system? Currently, two very different models of how self-replication might have been first achieved are on offer.¹²

One, the "metabolism-first" model,¹³ envisages that the first self-replicating system consisted of what Stuart Kauffman calls a "collectively autocatalytic set" (CAS): a large set of molecules that have the collective ability to synthesize every member of the set.¹⁴ As described by Kauffman, in a CAS "every member of the autocatalytic set has at least one of the possible last steps in its formation catalyzed by some member of the set, and... connected sequences of catalyzed reactions lead from the maintained 'food set' to all members of the autocatalytic set."¹⁵ As Vera Vasas et al. comment: "The central thesis in this scenario was that template replication is not required to achieve an autocatalytic set."¹⁶

The alternative conception of the first self-replicating system is an RNA ribozyme (an RNA polymer capable of carrying out enzymatic syntheses) that can synthesize other ribozymes as well as itself.¹⁷

There are problems with both scenarios. As Kauffman remarks: "To date, only collectively autocatalytic DNA, RNA, and peptide sets [i.e., those seen in current cells] have achieved molecular reproduction of polymers."¹⁸ Still, he claims, "Theoretical work and experimental work on CAS... support their plausibility as models of openly evolvable proto-cells, if housed in dividing compartments such as dividing liposomes."¹⁹ Kauffman sees the sudden emergence of an autocatalytic set of molecules as occurring like a phase transition. He admits, however, that despite being theoretically well-grounded, the CAS model "awaits experimental proof using combinatorial chemistry to make libraries of stochastic DNA, RNA and/or polypeptides, or other classes of molecules to test the hypothesis that molecular polymer reproduction has emerged as a true phase transition in complex chemical reaction systems."²⁰ And just as no CAS has ever been synthesized, neither has any RNA molecule capable of complete self-replication.

Supporters of the CAS model see problems with the ribozyme model,²¹ and supporters of the ribozyme model see problems with the CAS model.²² As the authors of a recent paper comment: "[CAS supporters find it] improbable that RNA-like self-

replicating polymers appeared before natural selection had operated on chemical networks, whereas genetics-first supporters find implausible the idea that molecular networks without genetic control could have undergone Darwinian evolution.”²³ To date no RNA replicase, i.e., a template-dependent RNA synthetase capable of ... nucleotides, has been synthesized.²⁴ And even advocates of the RNA world concede: “The problem of the origin of the RNA world is far from being solved.”²⁵

Thus, as things stand today, there is no universally-agreed-upon route to the first replicating system. No one has synthesized a self-replicating RNA molecule or assembled a collectively autocatalytic set. The verdict is still out on these two competing hypotheses. No one knows if either of them is possible and would actually work.

c. The Genetic Code

Even if self-replication could have been achieved either via a CAS or RNA template route, no plausible scenario for the evolution of the modern DNA-protein genetic code, via gradual functional continuums of increasingly more complex cellular forms, has ever been developed. In a recent critical paper summarizing this current impasse in the origin-of-life field, Eugene Koonin and Artem Novozhilov comment:

At the heart of this problem is a dreary vicious circle: what would be the selective force behind the evolution of the extremely complex translation system before there were functional proteins? And, of course, there could be no proteins without a sufficiently effective translation system. A variety of hypotheses have been proposed in attempts to break the circle... but so far none of these seems to be sufficiently coherent or enjoys sufficient support to claim the status of a real theory.²⁶

About proto-protein synthesizing systems halfway to the modern cell they comment:

Nevertheless, these and other theoretical approaches lack the ability to take the reconstruction of the evolutionary past beyond the complexity threshold that is required to yield functional proteins, and we must admit that concrete ways to cross that horizon are not currently known.²⁷

I expressed similar sentiments in *Evolution: A Theory in Crisis*: “That such a cell [lacking an accurate means of replicating its constituents] might undergo further evolution, improving itself by ‘selecting’ advantageous changes which would be inevitably lost in the next cycle of replication, seems contradictory in the extreme.”²⁸

About the RNA world and the origin of the genetic code, Koonin and Novozhilov comment:

On the experimental front, findings on the catalytic capabilities of selected ribozymes are impressive... In particular, highly efficient self-aminoacylating ribozymes and ribozymes that catalyze the peptidyltransferase reaction have been obtained... Moreover, ribozymes whose catalytic activity is stimulated by peptides have been selected... hinting at the possible origins of the RNA-protein connection... Nevertheless, in a close analogy to the situation with theoretical approaches, we are unaware of any experiments that would have the potential to actually reconstruct the origin of coding, not even at the stage of serious

planning.²⁹

Summarizing the state of the art, they conclude:

We cannot escape considerable skepticism. It seems that the two-pronged fundamental question: “why is the genetic code the way it is and how did it come to be?” that was asked over 50 years ago, at the dawn of molecular biology, might remain pertinent even in another 50 years. Our consolation is that we cannot think of a more fundamental problem in biology.³⁰

d. Laws of Form

The failure of the current approach to provide a plausible account of the origin of the first cell in conformity with what Darwin referred to as the “law of continuity”³¹ strongly suggest that the development of the first cell might have been saltational, and involved novel self-organizational principles or properties of matter yet to be elucidated. This would imply that the pathway to the first cell was “built into the natural order” and the inevitable determined result of cosmic evolution.

That nature may indeed have “lent a hand” is conceded by Gerald Joyce, who, in discussing how the “clutter problem” might be overcome, speculates that the solution can only lie in special conditions or special synthetic paths which facilitated the route to the protocell:

Perhaps there were special conditions that led to the preferential synthesis of activated β -D- nucleotides or the preferential incorporation of these monomers into polymers. For example, the prebiotic synthesis of sugars from formaldehyde can be biased by starting from glyceraldehyde phosphate, leading to ribose 2,4-diphosphate as the predominant pentose sugar... The polymerization of adenyate, activated as 5'-phosphorimidazolidine, yields 2',5'-linked products in solution, but mostly 3',5'-linked products in the presence of a montmorillonite clay. *Thus through a series of biased syntheses, fractionations and other enrichment processes, there may have been a special route to a warm little pond of RNA.*³²

Joyce is surely right. There has to be a “facilitated natural path”; there have to be unique elements of fitness in nature to call forth life from chemistry. Time and chance and the currently known laws of chemistry and physics alone are certainly insufficient. In a similar vein, Itay Budin and Jack Szostak describe the ability of unexpected physical processes to facilitate the self-assembly and self-replication of the first biological systems:

Laboratory efforts have uncovered novel physical mechanisms for the emergence of homochirality; the concentration and purification of prebiotic building blocks; and the ability of the first cells to assemble, grow, divide, and acquire greater complexity. In the absence of evolved biochemical capabilities, *such physical processes likely played an essential role in early biology.*³³

Also, as they point out, membrane systems composed of fatty acids have many properties eminently fit to act as spontaneously self-assembling cell membranes in primitive cell systems.

An important point seldom highlighted in origin-of-life debates is that both the

autocatalytic set model (metabolism first) and the self-replicating RNA model (template first) are, strictly speaking, “non-Darwinian” models. Consider the CAS model. There is no functional continuum leading to the magic moment when a CAS is achieved. On the contrary, the transition of a soup of chemicals into a collectively auto-catalytic set is a sudden saltational event akin, as Kauffman puts it, to a “phase transition.”³⁴ Similarly, there is no gradual functional continuum leading to the magic RNA self-replicator. An RNA either self-replicates or it does not.

Again, the existence of an RNA world is only conceivable because nature has provided in RNA a molecule carrying genetic information and the ability to copy itself. The same is true of the potential of a soup of chemicals to possess autocatalytic capabilities. Either route would have to be, as it were, “built into nature.” Darwinian evolution may well apply *after* self-replication is achieved, but if that achievement was the result of either of the two competing hypotheses, then selection could have played no role in the actualization of the primordial replicator.

Supportive evidence that the origin of life may have been prefigured into the order of things comes from work which indicates that the genetic code is better than a vast number of alternative coding systems at minimizing the effects of translational error on protein functions. It is even claimed by some authors that the “canonical code is at or very close to a global optimum for error minimization across plausible parameter space.”³⁵ Just how it became optimized to minimize translation error is not clear. Although there are some alternative codes which do outperform the canonical code in minimizing translational errors,³⁶ the canonical code also appears to be optimized for another different function: the embedding within protein coding sequences of additional regulatory and control sequences. This phenomenon was reported in a paper from Uri Alon’s group at the Weismann Institute in Israel:

DNA sequences that code for proteins need to convey, in addition to the protein-coding information, several different signals at the same time. These “parallel codes” include binding sequences for regulatory and structural proteins, signals for splicing, and RNA secondary structure. Here, we show that the universal genetic code can efficiently carry arbitrary parallel codes much better than the vast majority of other possible genetic codes... Whereas many of the known regulatory codes reside in nontranslated regions of the genome, the present findings suggest that protein-coding regions can readily carry abundant additional information.³⁷

If the embedding of additional sophisticated overlapping control sequences—such as RNA splicing signals and protein binding sites—became adaptive only long after the structure of the code was initially fixed (as seems likely), then it would appear that the code was pre-adapted to serve the needs of later, more advanced cell systems. Moreover, Alon’s work raises the possibility that the code is optimized not just for minimizing translational errors and for parallel coding, but for other adaptive ends yet to be elucidated. This intriguing evidence is obviously consistent with the notion that nature is prefigured or fine-tuned not only to generate the wonderfully fit—perhaps, ideally and uniquely fit—canonical code, but other core features of the cell as well.

In a recent paper, pointedly entitled “Origin of Life Scenarios: Between Fantastic

Luck and Marvelous Fine-Tuning,” the authors comment on the “RNA world” hypothesis:

The proposed picture points to the existence of molecules capable of an amazing cascade of pairing, stacking, and self-association in ordered structures prone to chemical ligation, a set of properties that enabled self replication and hence life information storage. Certainly some of these properties were crucial in the selection of nucleic acids as the carrier of genetic information. The very existence of molecules embodying all these properties is not obviously deducible from the basic knowledge of organic chemistry. Furthermore, if this was indeed the pathway for the emergence of life, it was necessary that these properties were not shared by many other molecular species, so that RNA could have emerged without too strong a competition from molecules sharing similar properties. Hence, the proposed scenario points to a delicate fine-tuning of factors that we could name “marvelous” because (i) there is, rather surprisingly, a molecular species that shows all of them and (ii) because they are so delicately balanced to be extremely rare within the vast realm of molecular species. Both factors are certainly, but subtly, necessarily implied by the basic structure of matter (electron charge, proton mass etc.) and hence related to the basic architecture of the Universe.³⁸

The plausibility of the claim that nature lent a hand in calling forth life from chemistry is enhanced by the discovery of the extraordinary fine-tuning of the cosmos for life as it exists on earth and even for advanced life forms. (Consider the vast inventory of organics in space, the amazing fitness of water and the carbon atom for life on earth, and the fitness of nature for oxidative metabolism, which provides a unique energy source for organisms like ourselves.³⁹) And if the laws of nature are so fine-tuned for the generation of the “atoms of life” in the stars, for the synthesis of vast quantities of organics in space (including many of the basic monomers used in carbon-based life on earth, the first steps on the path to the cell), then it is surely not unreasonable to envisage that the fine-tuning is not just for the assembly of amino acids into polypeptides but also for the assembly of the first cell, and indeed, for the whole evolutionary progression of life on earth.

In this context, it is intriguing that Owen advocated “nomogeny”: life emerging by natural law.⁴⁰ By contrast, Darwin remained somewhat noncommittal as to how life had arisen. Although he did believe that life had arisen by natural processes, he had to his regret used the Pentateuchal term of life having been “breathed by the Creator into a few forms or into one” in the final sentence of the second and subsequent editions of the *Origin*.⁴¹ Being more forthright in advocating “origin by law,” Owen was able on this issue to appear to “out-naturalize Darwin.”⁴² It might seem curious in the context of what Ron Amundson called “Synthesis Historiography” (see Chapter 3) that any nineteenth-century structuralist should be depicted as an arch-naturalist. But as a believer in the origin of life by natural law, Owen saw the origin of life as analogous to the lawful a-historic process of crystallization⁴³—and therefore specified in the laws of nature from the moment of creation and an inevitable end of cosmic evolution. Thus, he even might be seen to “out-naturalize” many current origin of life researchers. And certainly if the “nomogeny” or “laws of form” paradigm is correct, then life throughout the universe should be based on the same basic plan and design as the cell system on earth, including even specific details such as the assignments of the genetic code.

The heroic effort to provide an account of life's origin in terms of a continuum of functional forms leading from chemistry to the cell has failed.⁴⁴ Despite a fantastic increase in knowledge in so many areas of biology, the deep enigma as to how life was drawn from chemistry remains unsolved. And the possibility that as-yet unknown natural organizational phenomena were responsible is simply impossible to refuse. The work of Uri Alon on the capacity of protein-coding sequences to encode additional information for various regulatory purposes hints very strongly that this is so—that at least the actualization of the code in the last common ancestor was no matter of chance.

7.2 The Enucleate Red Cell

One of the simplest of all the defining novelties of any major taxon is the enucleate red blood cell of mammals. This is a homolog shared by monotremes, marsupials, and placentals, and so must be assumed to be an ancient novelty which originated in the common ancestor of all extant mammalian species.

The terminal differentiation of the red cell in mammals involves two very different types of change. There is, firstly, a phase of continuous incremental change, leading over two to three days from the large nucleated erythroid stem cell through several cell divisions to the much smaller normoblast (the final cell type before the nucleus is ejected), during which time hemoglobin accumulates in the cytoplasm. Then there occurs a dramatic saltational event when the nucleus is ejected from the normoblast, resulting in the enucleate red blood cell.⁴⁵

This particular homolog holds a personal fascination for me reaching back to my days as a doctoral student. My PhD thesis in the Biochemistry Department of King's College, London, was on the development of the mammalian red blood cell.⁴⁶ The fact that the enucleation could hardly be explained by cumulative selection was very apparent to me as I was completing my doctorate. It struck me then, and still does now, that it is very difficult to envisage how the enucleate final state could have been achieved gradually by any sort of Galápagos-type, incremental adaptive change.

Cells cannot have a nucleus “half-in” and “half-out” of the cell. The intermediate position is not only unknown in the whole domain of nature, but is self-evidently unstable. There is no known functional continuum leading from a nucleated normoblast to the enucleate erythrocyte. So here is one of the defining traits of the class Mammalia that is definitely *not* led up by any known functional continuum.

In addition, the process is extremely complex.⁴⁷ Narla Mohandas, a leading researcher on the biology of the red cell, recently commented:

Enucleation is a multistep process... that requires displacement of the nucleus in the erythroblast to one side during the preparatory stage. This is followed by formation of a contractile actin ring, pinching off the nascent reticulocyte from the nucleus, and subsequent redistribution of membrane between the 2 lobes of the dividing cell by vesicle shuttling to restrict the area of contact between the 2 emerging cells. The coordinated execution of these diverse events during a period of 8 to 10 minutes requires complex machinery embracing a number of distinct cytoskeletal proteins and signaling interventions.⁴⁸

Despite a huge amount of research into the underlying mechanisms, much still remains to be clarified. Nonetheless, it is clear that much of the cell's basic cytological machinery is co-opted in absolutely unique ways to “push” the nucleus to the side and eventually out of the cell.

As the authors of a recent paper point out,⁴⁹ the process is similar to ordinary cytokinesis but differs in unique ways. Enucleation involves: (1) the formation of an actin cytoskeleton, which pushes the nucleus to one pole; (2) vesicular trafficking, creating asymmetric protein distribution in the cytoplasm; (3) protrusion of the plasma membrane surrounding the condensed nucleus along with the nucleus; and (4) accumulation of vesicles and vacuoles in the region between nucleus and cytoplasm and their coalescence into U-shaped channels, which facilitates the separation of the erythrocyte from the nucleus.

This is not all. Extrusion also involves complex changes to the membrane structure in the region where the nucleus is sited immediately before enucleation. As the authors explain: “The membrane that is destined to enclose [the] pyrenocyte [the extruded nucleus] that is in close proximity to [the] nucleus lacks actin cytoskeleton, spectrin, and other critical proteins and as a result can be visualized to balloon out without resisting the pressure exerted by the cytoskeletal activity.”⁵⁰ In other words, a unique reorganization of the plasma membrane surrounding the nucleus facilitates the extrusion process. Further, “Pyrenocytes gradually start expressing phosphatidyl serine on their surface, providing an ‘eat me’ signal for macrophages, which engulf them.”⁵¹

In another recent paper, the authors suggest that the process of pushing the nucleus to the side of the cell prior to extrusion resembles another process that occurs in migrating cells. Junxia Wang et al. comment:

Here we show that enucleation requires establishment of cell polarization that is regulated by the microtubule-dependent local activation of phosphoinositide 3-kinase (PI3K). When the nucleus becomes displaced to one side of the cell, actin becomes restricted to the other side, where dynamic cytoplasmic contractions generate pressure that pushes the viscoelastic nucleus through a narrow constriction in the cell surface, forming a bud.⁵²

Our results suggest that enucleation is carried out in a way mechanistically similar to directed cell migration. Some migrating cells form a polarized bleb-like protrusion in order to move forward... and the difference between the role of the bleb-like protrusion in cell migration and enucleation is probably influenced by differences in their cytoskeletal organization.⁵³

Enucleation is triggered and continued by a pressure generated by contractions of cytoplasmic actomyosin... and is probably completed by contractions of concentrated actomyosin at the bleb neck.⁵⁴

It is surprising that, after years of intense study of this unique phenomenon—one of the “simplest” of all the taxa-defining novelties in nature—Wang et al. can still remark that “most molecular events in enucleation remain unclear.”⁵⁵ This is a massive testimony to the extraordinary complexity of living cells and of this particular novel cytological process.

One thing is not in doubt: The entire cytoplasmic machinery of the cell—the cytoskeleton, vesicle trafficking and much more—is reorganized in unique ways to achieve the novel end of enucleation.

The enucleation of the red cell illustrates nicely one of the mantras of evo-devo, that Type-defining novelties involve few novel processes or elements, and mainly co-opt pre-existing elements of a “toolkit” (in this case made up of cytological elements) in unique combinations towards novel ends. Yes, established pre-existing cytological elements, mechanisms, and processes are co-opted. These include actin and myosin molecules, vesicles and vesicle transport, microtubules, intermediate fibers, spectrin and other membrane proteins, the formation of a contractile rim, the formation of a multi-vesicular “gap” between the nucleus and main remaining body of the cytoplasm, the change in the cell membrane structure round the nucleus, the connecting bleb full of actin fibers pushing the nucleus out of the cell, and other elements. But the unique way in which they are co-opted towards such a unique end provides not the slightest hint of an explanation of how the novel combination came about (see Chapter 5).

The whole remarkable “choreography of the red cell exit” poses a self-evident and obvious challenge to incremental functionalism. Between a nucleate and an enucleate cell is a quantum jump. There is no known intermediate type of cell midway between the enucleate mammalian red cell and the nucleated red cells of any other vertebrate species. And I think one can insist that such an intermediate cell (partially enucleate) never existed. Without intermediates (partially enucleate cells), there could be no way of approaching the enucleate state gradually via a functional continuum in which each increasingly “enucleate” cell is tested for its adaptive utility. And if there are no intermediates, then the utility of the enucleate red cell, if it is adaptive, could only have been tested when the enucleate cell enters the blood stream and is forced through the tiny capillaries. This means that the very first test of the utility of the enucleate red cell could only have been carried out *after* the complex and unique machinery for pushing out the nucleus was fully operational and already in place.

Even if one could invent some “just-so story” imputing selection for some function other than extrusion to account for the evolution of the complex cytoplasmic choreography, the final act would still be a saltation, so even on such a scenario, testing the utility of the enucleate state could not have occurred gradually. In fact, even if we allow cells with an eccentrically placed nucleus some stability so they could enter the circulation and survive for some time, almost certainly they would be maladaptive, and given that the delivery of oxygen to the tissues is one of the most fundamental of all physiological functions, almost certainly they would be selected against.

In the above discussion I have assumed that the final enucleate cell is actually adaptive, i.e., that the enucleate cell is better able to navigate the very narrow capillaries and hence deliver oxygen to the tissues more efficiently than a presumed ancestral nucleated cell. And this is how I viewed the enucleate cell while at King’s in the 1970s. As Narla Mohandas comments: “To fulfill the requirements of shape and flexibility, combined with mechanical stability, the nucleated precursor must dispose of its nucleus.”⁵⁶ This is the canonical adaptive explanation for enucleation. Ganesan Keerthivasan et al. make the same argument: “Mammalian erythrocytes extrude their nucleus prior to entering

circulation, likely to impart flexibility and improve the ability to traverse through capillaries that are half the size of erythrocytes.”⁵⁷ And Mohandas and Patrick Gallagher point out:

The structural organization of the human red cell membrane enables it to undergo large reversible deformations while maintaining its structural integrity during its 4-month sojourn in the circulation. The red cell membrane exhibits unique material behavior. It is highly elastic (100-fold softer than a latex membrane of comparable thickness), rapidly responds to applied fluid stresses (time constants in the range of 100 milliseconds), and is stronger than steel in terms of structural resistance.⁵⁸

But while there are clearly adaptive features to the design of the red cell, particularly the wonderfully engineered membrane, and it is possible that the enucleation of the red cell *may* have been an adaptive innovation at some period in the early evolutionary history of mammals, a number of considerations undermine the canonical account.

One widely touted adaptive explanation of the enucleate cell is that it promotes the iconic biconcave shape, which in turn provides a large surface area for gaseous exchange.⁵⁹ But this explanation does not play out in practice, for the cell in the capillary bed is deformed and does not adopt the iconic biconcave form where it matters! (The capillaries are half the diameter of the human red cell, so massive shape deformation is an inevitable consequence of passage through them.) In the early stages of mammalian embryogenesis, where the demand for oxygen is high and when the major species of hemoglobin have a higher affinity for oxygen than in adult mammals, *nucleated red cells* and far larger red cell precursors do enter the blood stream, and the mature enucleate fetal erythrocytes are considerably larger than those in the adult.⁶⁰

Even more challenging is the fact that red cells in birds, which have a higher metabolic need for oxygen than mammals, retain their nucleus. Anyone who has watched a hummingbird sucking nectar from a flower, with its heart beating sixty times per second, or watched geese flying over the Himalayas, under greatly reduced oxygen partial pressure at 8,000 meters, will have been struck by the incredible ability of birds to deliver oxygen to their muscles to empower flight. If birds get by with nucleated cells, perhaps the enucleate state is not quite as specifically adaptive for oxygen transport to the tissues as is widely assumed!

There are further considerations that suggest that the origin of this novelty (one of the defining novelties of the taxon Mammalia) is beyond any simple adaptive explanation. The size of the red blood cells in different species of mammals varies (see Figure 7-1) in ways that have never been accounted for in adaptive terms. In the case of mouse deer, the red cell is two microns across, less than a third of the diameter of a human red cell.⁶¹ Why, if the selection for enhanced ability of the red cell to traverse the smallest capillaries was the driving force that led to the loss of the nucleus, have our cells remained so large compared with those of a goat or a mouse deer? And what selection pressures can possibly explain the species-specific differences among extant mammalian species?

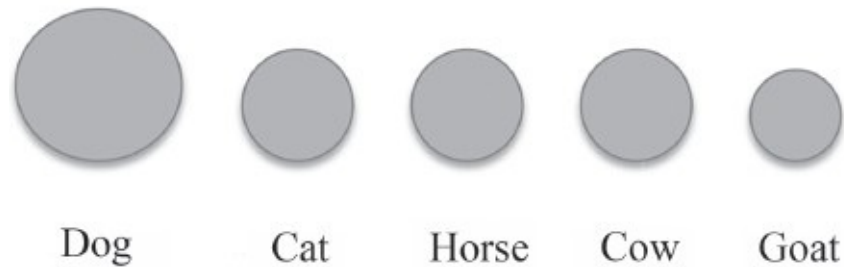


Figure 7-1. Relative sizes of Mammalian red cells.

So here is an enigma. A saltation event, occurring over eight to ten minutes, ejects the nucleus from a cell—a process involving a host of biochemical and cytological mechanisms, which necessitates re-engineering the entire cyto-architecture of the cell to that end. And so even if there were enigmatic adaptive reasons for this unique event in an early mammalian ancestor, accounting for its origin in terms of classic Darwinian incremental functionalism still breaks down because of the final saltational event—because the utility of the enucleate state cannot be tested via any conceivable intermediate cells mid-way between the enucleate and nucleated state.

Altogether, the enucleate cell poses a severe mix of challenges to functional incrementalism. Every aspect of this mystifying process points away from cumulative selection to deep and enigmatic internal causal factors at work in the origin of this taxon-defining novelty. Darwin himself conceded: “If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous successive slight modifications, my theory would absolutely break down.”⁶² Here is one! Here is a defining homolog, far simpler than almost any other, which still presents a massive roadblock in the way of simplistic Darwinian explanations.

7.3 The Origin of the Endometrial Cell Type

Another Type-defining novelty is the placenta. The placenta is unique to *placental mammals*. While there are other Type-defining differences between placental mammals and marsupial mammals (in dental formulae, in the mammary glands,⁶³ etc.), the placenta is perhaps the most significant.

An essential step in the establishment of pregnancy in placental mammals is the differentiation (decidualization) of the endometrial stromal cells (ESCs), a cell type unique to placental mammals.⁶⁴ This process involves the transformation of the spindle-shaped stromal fibroblasts (the progenitor cells) into the plump secretory ESCs prior to the implantation of the embryo. Decidualization of the ESCs is driven by hormonal changes associated with the menstrual cycle and involves extensive reprogramming of many cellular functions, including the simultaneous silencing of cellular proliferation pathways and activation of progesterone and cAMP signaling pathways. When implantation does not occur and pregnancy does not proceed, the endometrium lining of the uterus is shed or reabsorbed. Periodic degeneration and shedding of the endometrial lining (overt menstruation in many primates)⁶⁵ or its degeneration and reabsorption (covert menstruation in most other mammals) is a defining characteristic of the placental clade.

Some idea of the complexity of the cellular and physiological transformation involved in the differentiation of this novel cell type is gleaned from the list of changes

documented in a recent paper:

The most conspicuous aspect of this tissue transdifferentiation is a transformation of stromal cells into large, polyploid cells with epithelioid appearance. These decidual cells are characterized by an accumulation of glycogen and lipids in the cytoplasm, numerous lysosomes, large rough endoplasmic reticulum, as well as by extensive cell-to-cell contacts and junctional complexes, including gap junctions, desmosome-like junctions, and tight junctions... The differentiation of the endometrium into decidual tissue is called the decidual cell reaction (DCR) or decidualization, and it also involves several changes in extracellular components, such as reduction of intercellular space and remodeling of its matrix with a decrease in the number of collagen fibrils.⁶⁶

In the same paper the authors document several hundred changes in gene expression:

We found 322 annotated genes exhibiting significant differences in expression... of which 312 have not been previously related to decidualization. Analysis of overrepresented functions revealed that protein synthesis, gene expression and chromatin architecture and remodeling are the most relevant modified functions during decidualization. Relevant genes are also [involved in]... differentiation, cell proliferation and signal transduction.

It is not surprising that the differentiation of such a complex cell type involves so many different changes in gene expression. And an obvious question arises: Did these changes occur in Darwinian fashion, one gene at a time, i.e., gene one, gene two, gene three, up to gene 322? Or might the unique gene expression pattern associated with decidualization have originated from internal causal factors *per saltum*?

From first principles, it is difficult to see how the complex biochemical changes involved would have had any selective advantage relevant to implantation of the embryo until the full suite of changes (or at least a majority of the changes) was already in place. It is hard to believe that the various proteins and other biochemicals synthesized in the ESC—including prostaglandins, hyaluronate, prolactin-like proteins, desmin, vimentin, catechol-O-methyltransferase, ornithine decarboxylase, and alkaline phosphatase⁶⁷—could have been of any adaptive utility individually in preparing the uterus for implantation. Recent studies have shown that desmin, laminin, vimentin, hyluronate and alkaline phosphatase (which are synthesized by the ESCs) are all essential functional components of the endometrial stroma.⁶⁸ A *per saltum* origin would make physiological sense!

Further evidence that the differentiation of the ESC is associated with alterations in considerable numbers of gene circuits comes from a fascinating recent analysis by Günter Wagner's group at Yale of the rewiring of the genetic regulatory circuits that accompanied their evolutionary origin. As they acknowledge in a recent *Nature Genetics* paper,⁶⁹ one of the fundamental challenges in biology is providing an explanation for the origin of *novelties* such as new cell types. In an attempt to elucidate the likely complexity of the new gene circuits and novel gene expression patterns associated with the origin of a novel cell type they documented the genetic changes associated with the evolution of the ESC. They “found that 1,532 genes were recruited into endometrial expression in placental

mammals, indicating that the evolution of pregnancy was associated with a large-scale [unique] rewiring of the gene regulatory network.”⁷⁰

But Wagner’s study also turned up something unexpected and potentially of great significance regarding the rewiring, something which hints that the origin of these cells might have occurred as the result of sudden saltational events in the early evolution of the mammals, as inferred above on purely functional grounds. Their study showed that about thirteen percent of the newly recruited genes are within a relatively short stretch of DNA from a unique transposon element⁷¹ referred to as MER20. They also showed that this special class of MER20 transposons binds transcription factors essential for pregnancy and coordinately regulates endometrial stromal cell gene expression throughout the genome. In a later paper they comment:

TE [transposon element]-mediated rewiring of gene regulatory networks is an attractive alternative to the gene-by-gene origination of *cis*-regulatory elements because it provides a mechanism to rapidly distribute nearly identical copies of regulatory elements across the genome that are capable of responding to the same input signals.⁷²

They go on to point out:

Taken together, our data suggest that novel gene regulatory networks and cell-type identities can evolve through large-scale genome-wide changes rather than gradual gene-by-gene changes... TEs may play a particularly important role in this process because they provide a mechanism to coordinately regulate the expression of numerous genes to the same stimuli upon their integration into multiple locations in the genome, alleviating the need for the *de novo* evolution of *cis*-regulatory elements capable of directing stereotyped responses to the same stimuli one gene at a time across the genome.⁷³

The evidence they present does not amount to a proof of a non-Darwinian origin of the transposon regulatory network, but it is very suggestive. They conclude in their *Nature Genetics* paper:

It is questionable whether the origin of complex novelties—such as the origin of new cell types, which involves the recruitment of hundreds of genes—can be achieved by... small-scale changes. Our findings indicate that the gene regulatory network of ESCs was rewired in placental mammals during the evolution of pregnancy, a reorganization partly mediated by the transposable element MER20. Furthermore, MER20s coopted specific signaling pathways essential for implantation and pregnancy into ESCs by acting as cell type specific regulatory elements. These findings strongly support the existence of transposon-mediated gene regulatory innovation at the network level, a mechanism of gene regulation first suggested more than forty years ago by McClintock and Britten and Davidson. Our data and those of other recent studies show that transposable elements are potent agents of gene regulatory network evolution and add to an increasing body of evidence indicating that *the evolution of novel characters involves genetic mechanisms that are distinct from those involved in the modification of existing characters.*⁷⁴

Of course, these are early days, and a great deal of further research will be necessary to establish the actual mode of origin of the unique gene circuits which led to the ESC. But as things stand, there is no evidence to support the notion that this defining novelty of placental mammals—the endometrial stromal cell—evolved in Darwinian fashion via a long series of adaptive intermediate cells. The evidence is certainly compatible with a saltational origin for this particular cell type, another taxon-defining homolog. And if it was by saltation, then again internal causal (structural) factors rather than cumulative selection would seem to have played a significant role.

7.4 The Origin of ORFan Genes

Perhaps the simplest of all novelties or homologs in nature are new functional protein-coding genes. New functional genes have been originating throughout the descent of living things from the last common ancestor of all life on earth nearly four billion years ago, as genomes have expanded from a few hundred genes in viruses, to a few thousand in bacteria, to up to twenty thousand in complex organisms like extant vertebrates. How have new functional genes come about? Again, it seems that a remarkable proportion of these novelties have originated *per saltum* (by leaps) and not by gradual cumulative selection.

For many decades, in conformity with Darwin’s “law of continuity,” it has been assumed that new gene functions “evolve” gradually from preexisting genes. Supposedly, a gene duplicates, and then the new copy, being free from the functional constraints on the old ancestral gene sequence (which prevent its undergoing sequential divergence and acquiring a new function) is able to undergo gradual Darwinian functional evolution until a new function is established. As the authors of a recent *PLoS Genetics* Perspective comment: “For a long time the answer to that question [where do new genes come from] has simply been ‘from other genes’... [by] gene duplication in all its guises: exon shuffling, tandem duplication, retrocopying, segmental duplication, and genome duplication.”⁷⁵

This was the paradigm until a few years ago. As recently as 2003, papers were still extolling the notion:

It can be expected that, with an explosive increase in genomic data and rapid advances in molecular genetic technology, the manifold and fundamental roles of gene duplication will become even more evident and the once imaginative idea of evolution by gene duplication *will be established as one of the cornerstones of* [Darwinian] evolutionary biology.⁷⁶

The alternative notion of *de novo* gene origination had been deemed very unlikely because of the seeming vast improbability of a functional gene sequence emerging from a random sequence. Adam Siepel listed some of the complex changes necessary to transform a non-coding sequence into a protein-coding sequence:

While a single gene is not as complex as a complete organ, such as an eye or even a feather, it still has a series of nontrivial requirements for functionality, for instance, an ORF [open reading frame], an encoded protein that serves some useful purpose, a promoter capable of initiating transcription, and presence in a region of open chromatin structure that permits transcription to occur. How could all of these pieces fall into place through the random processes of

mutation, recombination, and neutral drift—or at least enough of these pieces to produce a protogene that was sufficiently useful for selection to take hold?⁷⁷

Consequently,

the origination of protein-coding genes *de novo* from nonrepetitive, noncoding DNA has been thought to occur only as an exceptionally rare event during evolution. Indeed, the emergence of complete, functional genes—with promoters, open reading frames (ORFs), and functional proteins—from “junk” DNA would seem highly improbable, almost like the elusive transmutation of lead into gold that was sought by medieval alchemists.⁷⁸

Other researchers have alluded to further changes that would have to be made:

Conversion from noncoding to coding seems too unlikely an event to happen in a single evolutionary step. The sequence in question must be transcribed, escape degradation at the nuclear exosome, associate with ribosomes, be translated, and again escape degradation by the proteasome. Finally, it must avoid toxic conformations such as amyloid, for example, in favor of a stable protein fold.⁷⁹

Obtaining a new functional gene sequence from scratch would certainly seem to be highly improbable.⁸⁰ The complexity of functional gene sequences and their likely rarity in sequence space has been the subject of a great deal of recent research.⁸¹ Yet, despite the experimental evidence and theoretical considerations which suggest that the emergence of functional genes in non-coding sequences by “chance” leaps would be vastly improbable, there is now, *against every Darwinian expectation*, “a growing appreciation of the oft-dismissed possibility of evolution of new genes from scratch (i.e., *de novo*) as a rare but consistent feature of eukaryotic genomes.”⁸² Siepel calls this the “alchemist’s sorcery.”⁸³

Genes that are ORFans (a play on Open Reading Frame) are “orphans” because they have no homologues in other organisms. In other words, they are taxonomically restricted. As genomic sequencing continues, more and more ORFan genes are being found. Indeed, incredible as it might seem in the context of the Darwinian framework, it appears that all genomes contain ORFan genes, and further, that the proportion of all protein-coding genes which originated *de novo* from non-coding sequences is between ten percent and twenty percent and may be as high as thirty percent.⁸⁴ Evidence presented in a recent paper⁸⁵ shows that the proportion of all genes that are taxonomically restricted is increasing as the number of genomes is sequenced. As data is accumulating, it seems that more and more genes are turning out to be ORFans. This implies that a very significant proportion of all functional genes emerged in the course of evolution *de novo* from non-coding sequences *and not by gradual cumulative selection from other functional genes as Darwinism predicts*.

One final and fascinating twist to the ORFan gene phenomenon is a highly intriguing observation made by the authors of a recent paper, that in *Hydra*, ORFans appear to be “play[ing] a role in the creation of phylum-specific novelties such as cnidocytes, in the generation of morphological diversity and in the innate defence system. We propose that taxon-specific genes drive morphological specification, enabling organisms to adapt to changing conditions”⁸⁶ In the case of *Hydra*, morphological and cellular novelties appear to utilize novel genes that have no direct genetic antecedents. While taxa-defining

novelties may on the whole be the result of reshuffling and reuse of pre-existing genes and gene circuits (as discussed in Chapter 5) at least some *novel* genes may also be involved, as appears to be the case in *Hydra*. And if the genes arose *per saltum*, this supports the notion that the taxa-defining novelties themselves may also have arisen suddenly in concert with the genes, rather than gradually through a series of intermediate forms.

That new protein-coding genes can originate *de novo* is certainly one of the most “unexpected tales” of the new era of genomics. Moreover, as genomic comparisons become ever more sophisticated and as more and more genomes are sequenced, it is increasingly apparent that *de novo* origination may have been a major route to new genes throughout the history of life. The terms used by researchers in the field—terms such as “enigmatic,”⁸⁷ “mystery,”⁸⁸ “unclear,”⁸⁹ and other such expressions of amazement—capture something of the challenge the ORFans are seen to pose to traditional gradualistic notions of gene evolution.

7.5 Summary

No matter how anomalous it may seem in the context of an evolutionary worldview firmly wedded to the notion of continuity, in the case of the eukaryotic red cell, the ESC, and ORFan genes, there is not the slightest evidence that they were actualized gradually via functional continuums as Darwinism demands. And while selection may have played *some role* in the actualization of these novelties, on any consideration of the evidence available, it surely cannot have been the main or even a major generative causal factor.

On the contrary, the evidence reviewed above provides overwhelming support for the radical structuralist notion that a considerable degree of organic order is the result of internal causal factors intrinsic to living systems. And in the case of the first self-replicating system and of the genetic code, again there is no evidence for believing that they came about gradually via adaptive continuums. The structuralist notion that natural organizational properties of matter may have played a crucial role is again impossible to refuse.

8. Bridging Gaps: Flowering Plants

The beautiful configurations produced by the orderly arrangement of leaves or florets on a stem have long been an object of admiration and curiosity... The spiral leaf-order has been regarded by many learned botanists as involving a fundamental law of growth, of the deepest and most far-reaching importance... We come then without more ado to the conclusion that while the Fibonacci series stares us in the face in the fir cone, it does so for mathematical reasons; and its supposed usefulness, and the hypothesis of its introduction into plant structure through natural selection, are matters which deserve no place in the plain study of botanical phenomena.

D. W. Thompson, *On Growth and Form* (1945), Chapter 14.

In *Evolution: A Theory in Crisis*, I wrote that “the sudden appearance of the angiosperms is a persistent anomaly which has resisted all attempts at explanation since Darwin’s time.”¹ The situation is little changed today. None of the taxa-defining characteristics of angiosperms, including the key novelties of the flower—sepals, petals, stamens, carpels—are found in any group of plants, extant or fossil,² outside of the angiosperm clade.³ Further, no putative ancestral group has been identified in the fossils or by molecular phylogenetics.⁴

As one author conceded, despite many recent paleontological and molecular advances, the evolutionary pathway which led from the putative ancestral seed-plant to the first angiosperms is still obscure: “No taxon [is] universally accepted as transitional between angiosperms and any other group.”⁵ And speaking for many researchers in this area, Peter Endress and James Doyle commented in a recent review:

The question of the structure and biology of the ancestral angiosperms, and especially their flowers, is an enduring riddle. Although we are continually gaining new insights from new fossils and new studies on phylogeny, morphology, and developmental genetics in extant plants, we are still far from a final answer. There are gaps at different levels. First is the uncertainty concerning which other seed plants are the closest relatives of angiosperms, particularly extinct groups *because most molecular analyses indicate that no living group of gymnosperms is any closer to angiosperms than any other*. Second, even if known fossils can be recognized as angiosperm stem relatives, all such groups are *morphologically well removed from angiosperms*, so there is still a major gap that can only be filled by the discovery of closer stem relatives. Third is the problem of the *original morphology and early evolutionary differentiation of crown group angiosperms*.⁶

In passing, it is worth noting that the angiosperms are not the only group of land plants that appear in the fossil record without antecedents. The same is true of many other groups of plants.⁷

A great deal is now known regarding the developmental genetics of the flower,

including the basic so-called “ABC developmental system.”⁸ It is also clear, as in the case of so many other novel homologs, that it was the recruitment of pre-existing gene circuits and pre-existing parts in angiosperm ancestors that led to the formation of the flower.⁹ But again, as in the case of the limb and the feather, such new “evo-devo” insights provide no real hint as to what causal mechanisms actualized the flower and *no* support for the notion that it came about “Galápagos fashion,” via thousands of tiny adaptive steps over millions of years. Just about all that developmental genetics tells us about the origin of the angiosperm flower is that pre-existing gene circuits were re-wired to make the flower, i.e., that angiosperms originated by descent with modification from some putative ancestral plant. But this has been assumed by almost all biologists since at least the middle of the nineteenth century.

Simply put, the angiosperm flower *Bauplan* is not led up to gradually via a series of transitional forms in any known extant or fossil plants. Not only are there no transitional forms, but to my knowledge, there does not appear to exist anywhere in academic botanical literature even a tentative hypothetical Darwinian functionalist scheme showing how the flower *Bauplan* or any of its defining homologs—sepals, petals, etc.—might have emerged via a series of tiny adaptive steps from some ancestral reproductive organ (presumably in a hypothetical gymnosperm). The current evidence is compatible with the possibility that the angiosperms originated *per saltum* or as a result of a series of major steps (as occurred in the evolution of the feather¹⁰) resulting from intrinsic self-organizing mechanisms in putative ancestral species. Günter Wagner has suggested two steps: step one, involving the unification of both male and female organs on the same shoot axis (in the more primitive gymnosperms the reproductive organs are separate); and step two, “integrating subdenting leaves as the perianth into the flower.”¹¹ But again, just what conceivable adaptive continuums could have led gradually, Darwinian-fashion, to the flower via these two steps is not easy to imagine. It is far easier, as in so many other instances, to envisage the “steps” as having an intrinsic developmental rather than an extrinsic adaptive cause.

8.1 The Origin of the Angiosperm Clades

The absence of any transitional forms linking the angiosperms to any putative ancestral clade and the absence of any plausible functionalist narrative explaining how the angiosperm *Bauplan* originated is only the beginning of the challenge to Darwinian notions posed by this wonderfully diverse group of plants. Since the angiosperms first emerged about 140 million years ago, they have diversified into a vast number of subgroups comprising about 250,000 different species.¹² And as Michael Sanderson reminds us, it is not just the origin of the angiosperms which is still an abominable mystery: “A number of much more recent clades of angiosperms could be interpreted as mini-abominations: That is, they have poor fossil records at their base, novel innovations with unclear transitional forms among related taxa.”¹³

On any reading of what is one of the most comprehensive recent publications in this area, Louis Ronse De Craene’s *Floral Diagrams*¹⁴—a book which contains several hundred floral diagrams and formulae for all the major angiosperm groups—it is clear that the domain of the angiosperms is one of discontinuities which cry out for internalist structuralist explanations that go far beyond incremental functionalism. Ronse De

Craene's book highlights the fact that the angiosperms, no less than the insects or any other major Type, can be classified into a hierarchy of increasingly more inclusive groups in which the diversity of each group is constrained by an underlying unique *Bauplan* or ground plan.

What makes the angiosperms so special is the extraordinary “merism” that characterizes the ground plans of the angiosperm subclades, perhaps more intensely than in any other major group of organisms. As Ronse De Craene explains:

Merism (or merosity) refers to the *number of parts per whorl in the flower* (usually based on petals or perianth, taken as reference). Merism is either indefinite, but more commonly trimerous [having flower parts in sets of three] or dimerous [having flower parts arranged in groups of two] (basal angiosperms, basal eudicots, monocots), or pentamerous [where each floral whorl consists of five parts—se-pals, petals, etc.] and tetramerous [having flower parts arranged in groups of four] (core eudicots). Merism is a major feature affecting the *Bauplan* of flowers besides symmetry and phyllotaxis... Trimerous flowers... are widespread in basal angiosperms and monocots. A derivation from a spiral condition is the most plausible interpretation for their origin... Dimery has arisen repeatedly by loss of a sector in each whorl of a trimerous flower, sometimes resembling a tetramerous flower... Origins of pentamery are not well understood, although five-merous flowers are found in the majority of angiosperms... Postulated origins of pentamery are a derivation from trimerous flowers (by amalgamation of two whorls)... or from spiral flowers.¹⁵

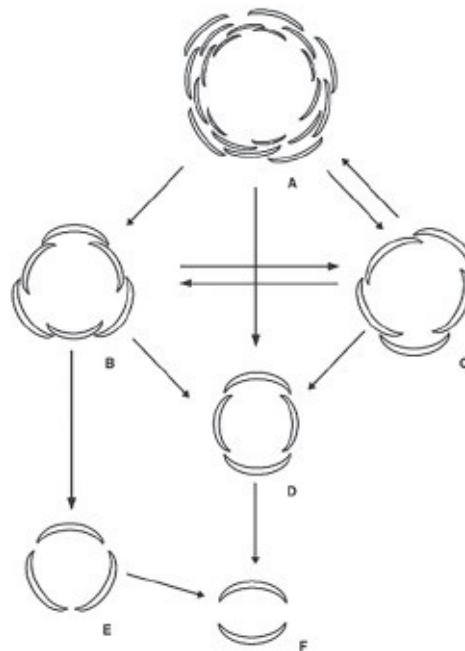


Figure 8-1. Relationships of Merism in the Perianth of Angiosperms. Undifferentiated perianth shown. (A) spiral with variable number of tepals; (B) trimery/hexamery; (C) pentamery; (D) dimery/ tetramery; (E) trimery, single whorl; (F) dimery, single whorl. [Reprinted from Louis P. Ronse De Craene, *Floral Diagrams: An Aid to Understanding Flower Morphology and Evolution* (Cambridge: Cambridge University Press, 2010), 30, Figure 1.5.]

The passage just quoted, along with the accompanying diagram (Figure 8-1) captures the core challenge to Darwinian incremental functionalism posed by the angiosperm universe. It is not that one pattern cannot be plausibly derived from another (via descent

with modification); the problem is that deriving one pattern from another involves saltational meristic changes which lie completely outside the domain of incremental functionalism. It may well be the case that each “meristic change” which persisted after its origin served some functional end (even if the specific end is hard to identify), but the primary causation of the actual emergence of a new meristic pattern could hardly have been incremental functionalism.¹⁶

8.2 On Growth and Form

The conception that the flower *Bauplan* originated as the result of intrinsic self-organizing processes and not as the result of external environmental functional constraints is by no means heterodox. It is widely acknowledged that the alternative spiral and whorled phyllotactic patterns witnessed in the positioning of leaves around a stem or shoot are the result of “laws of form” and arise spontaneously out of spacing of primordia and rates of growth.¹⁷ Henrik Jönsson et al. comment:

The beautiful symmetries apparent in phyllotaxis and its connection to mathematics have inspired scientists to create theories and models to explain these patterns. One important finding from mathematical analysis and physical simulation... is that many of the seemingly complex phyllotactic patterns and transitions found in plants can probably be explained to a large degree by any regular spacing mechanism superimposed on a gradually enlarging generative region.¹⁸

If self-organization accounts for the positioning of leaves on a stem, it is hard to refuse the possibility that analogous mechanisms may have been responsible for the origin of the flower and the derivation of the *Bauplans* of each major subgroup. Support for this notion comes from a very recent paper by two Japanese researchers, which raises the intriguing possibility that the common pattern of four or five sepals and petals in eudicots (the clade to which most angiosperms belong) may result from self-organizing processes in the developing flower. As the authors summarize their view:

We propose a development-based model of floral organ-number determination, improving upon earlier models of plant phyllotaxis that assumed two developmental processes: the sequential initiation of primordia in the least crowded space around the meristem and the constant growth of the tip of the stem. By introducing mutual repulsion among primordia into the growth process, we numerically and analytically show that the whorled arrangement emerges spontaneously from the sequential initiation of primordia... These results suggest that the temporal decay of initiation inhibition and the mutual repulsion among growing organs determine the particular organ number during eudicot floral development.¹⁹

8.3 Gametophyte Ontogeny

The whorls and spirals of the angiosperm flower *Bauplan* and the myriads of unique floral formulae characteristic of particular species are not the only features of angiosperm biology that challenge Darwinian functionalism. Another set of challenges arises from the far less familiar (and more bizarre) succession of cell divisions and nuclear movements which lead from the megaspore to the female gametophyte or embryo sac and onward to

the subsequent fertilization of the egg and formation of the endosperm.²⁰

The most common developmental pattern leading from the female megaspore to the female gametophyte is the so-called “polygonum” type. This commences with a diploid megaspore mother cell (see Figure 8-2), which undergoes meiosis to produce four haploid “daughter” mega-spores. Cell walls develop around the nuclei formed after the first meiotic division and around the four nuclei resulting after the second meiotic division. Next, three of the “daughter” megaspores undergo apoptosis (i.e., programmed cell death). The lone remaining megaspore then undergoes three successive mitotic divisions to produce eight haploid nuclei, which make up the female gametophyte and are enclosed within what is termed the “embryo sac” (see Figure 8-2). The eight haploid nuclei in the embryo sac are arranged in precise positions. Cell walls form around the nuclei to produce seven cells, which constitute the mature gametophyte (see Figure 8-3). The egg cell is located near the opening of the embryo sac. A large central cell contains the two central nuclei. Two cells called synergids flank the egg cell; and three other cells called the antipodals are located at the other end of the embryo sac, opposite the egg cell.²¹

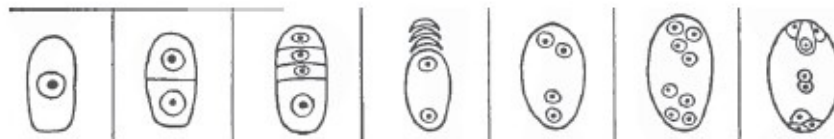


Figure 8-2. Maturing Gametophyte. The sequence of cytological events leading from the megasporangium to the mature gametophyte (the polygonum type). From left: first column represents diploid megasporangium; second and third columns show meiotic divisions leading to four haploid megaspores, each surrounded by a cell membrane, three of which undergo apoptosis, leaving one haploid megaspore; fourth, fifth and sixth columns show the haploid cell undergoing three rounds of mitosis, resulting in eight haploid nuclei; the final column shows cell walls forming around the three antipodal cells and the two synergids and the egg cell.

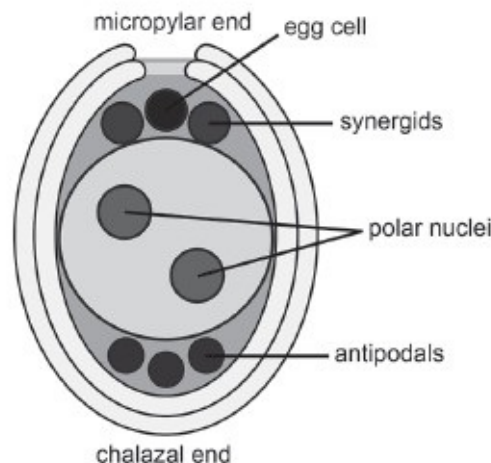


Figure 8-3. The Cytological Layout of the Mature Egg Sac.

A host of questions arise. What series of incremental functional changes dictated that three cells should die? Explaining features of angiosperm reproduction by reference to the putative ancestral gymno-sperm and more primitive seed plants just pushes the numeric problems back in evolutionary time.²² Again, I am not arguing that these curious patterns could not have arisen by descent with modification from earlier plant species, but I am insisting that they could not have arisen gradually via long sequences of tiny advantageous mutations.

It is particularly the variations on this standard pattern that challenge incremental functionalism and the Darwinian notion that *all* biological order is the result of externally imposed constraints to serve specific environmental necessities.

The polygonum “standard pattern” is termed “monosporic” because just one megaspore cell survives, which contains one haploid nucleus. In “bisporic” species, cell plate formation occurs only after the first meiotic division (meiosis 1), and results in two, two-nucleate megaspores, of which one degenerates, leaving one megaspore containing two haploid nuclei. The “tetrasporic” pattern, however, is characterized by the failure of cell plates to form after either meiosis 1 or 2, and results in one mega-spore containing four haploid nuclei. (Variations on these three patterns are illustrated in the seven rows of Figure 8-4.)

Each of the above-mentioned ontogenic patterns or trajectories gives rise to a single functional megaspore, which contains one, two, or four haploid nuclei, respectively. The megaspore then undergoes gametogenesis to give rise to the female gametophyte or embryo sac. This involves in the case of monosporic species three mitotic divisions, in the case of bisporic species two mitotic divisions, and in the case of tetrasporic species one mitotic division. Curiously, the result is that in many species, the embryo sac and the distribution of the nuclei within it is *the same* (see the far right column of the first three rows in Figure 8-4). So the three different patterns of divisions and nuclei migrations lead to the same end. What mystifying adaptive continuums could have generated such very different pathways to the same end?

And this is not the end of the variation. In just one small group of plants—the peppers—there are at least seven variations on this weird cytological choreography.²³


















































Type	Megasporogenesis			Megagametogenesis			
	Megaspore mother cell	Division I	Division II	Division III	Division IV	Division V	Mature embryo sac
Monosporic 8-nucleate Polygonum type							
Monosporic 4-nucleate Oenothera type							
Bisporic 8-nucleate Allium type							
Tetrasporic 16-nucleate Peperomia type							
Tetrasporic 16-nucleate Pennisetum type							
Tetrasporic 16-nucleate Drusa type							
Tetrasporic 8-nucleate Fritillaria type							

Figure 8-4. Cell Division in Peppers. The meiotic and mitotic divisions which lead to the female gametophyte in peppers. Columns two and three: the result of meiosis (division 1 and 2). Columns four, five, and six: the results of successive mitotic divisions.

On any consideration of these diverse series of cytological events, it is clear that causal factors in addition to cumulative selection must have been involved. None of the patterns shown can be derived from each other by anything remotely resembling Darwin’s insensible series of tiny adaptive steps, or everyday micro-variations. Moreover, the

“dance of the angiosperm nuclei” must necessitate underlying cytological machinery of very great complexity—vastly more complex than that in an individual red cell. Trying to envisage their origins via long functional continuums defies all reason.

Perhaps the only aspects of this weird choreography that do have some adaptive significance are the level of ploidy, and consequently the level of genetic heterogeneity of the central cell (which after fertilization develops into the endosperm, an organ which provides nutrition to the developing seed)²⁴ and the different contributions from the male and female parent.²⁵ But even if the different levels of ploidy in the endosperm have some adaptive significance, this is an adaptive exception which proves the rule: the generation of the female gametophyte in angiosperms, particularly the variation in the pattern of cell divisions leading from the megaspore to the mature gametophyte, is beyond any incremental functionalist explanation.

8.4 Fertilization

The baroque nature of the reproductive process does not stop with the series of cell divisions leading to the embryo sac. After the formation of the female gametophyte, the next stage in the life cycle of the angio-sperm is the fertilization of the egg. Fertilization occurs when the pollen tube reaches the embryo sac. Each pollen tube contains two sperm (both haploid, i.e., $1n$).²⁶ In the “standard model” (polygynum) one sperm cell fertilizes the egg cell so that a diploid zygote ($2n$) is formed, from which the embryo develops. The other sperm cell fertilizes the large central cell, in the middle of the embryo sac, which joins the two polar nuclei, each of which is haploid ($1n$). This gives rise to a $3n$ cell, which develops into the endosperm. This bizarre double fertilization event is unique to angiosperms.

The complexity of the events that lead to double fertilization, which is described by Valayamghat Raghavan,²⁷ simply beggars belief. The movement of the second sperm nucleus to the center of the embryo sac requires directing cytological mechanisms. Moreover, as in the case of enucleation of the red cell, this cell architecture must have already been in place before the union of the sperm with the two polar cell nuclei could have occurred. In effect, the $3n$ state could only have been tested for its adaptive utility after these complex directive processes were in place. Some idea of their complexity is conveyed in this passage from Raghavan’s review:

The journey of the two sperm deposited in the degenerating synergid to align with the egg and the polar fusion nucleus [the two nuclei in the center of the egg sac] respectively, is considered an arduous one and some attention has been paid to the mechanism by which this is accomplished. It is well-established that only the sperm nuclei fuse with their female reproductive targets; the rest of the pollen tube discharge and the sperm cytoplasm remain trapped in the milieu of the synergid. Two aggregates of actin filaments designated as “coronas” that presumably guide the pathway of the male gametes have been identified within the embryo sac of tobacco. One of the actin aggregates forms at the chalazal end of the degenerating synergid, extending from its middle lateral region to the region of the egg. The second band occurs in the interface between the egg and the central cell and extends from the side of the egg to the region of the polar nuclei.²⁸

Every stage seems even more baroque than the previous. Take the way that the sperm nucleus enters the embryo sac. What series of small adaptive steps led to the necessity for the second sperm to enter the degenerating synergid before tracking to and fusing with the central cell nuclei? Why does the synergid have to degenerate and why does the sperm have to enter the synergid in the first place? Put simply, *if these extraordinary events leading from the megaspore to the development of the female gametophyte and fertilization of the two nuclei polar cell had not been described, no one would believe them.*

8.5 Summary

In the end, no plausible Darwinian narrative can be invented to account for the origin and diversification of the angiosperms. It is simply impossible to believe that either the merism of the flower *Bauplans* or the weird dance of the nuclei in the formation of the egg sac arose to serve specific environmental constraints. The patterns actualized in this remarkable clade are far more readily explained in terms of intrinsic or internal self-organizing processes, even if at present the “laws of form” which generated this universe of beautiful patterns remain to be elucidated. To explain the numeric and geometric patterns which permeate all aspects of angiosperm biology in terms of incremental functionalism, i.e., “Darwinian order imposed from without,” leads only, as in so many other instances, to William Bateson’s “endless absurdities.”

9. Bridging Gaps: Limbs, Feathers, Wings, and Eels

[Nature] has advanced with slow and stately steps, guided by the archetypal light... from the first embodiment of the Vertebrate idea under its old Ichtyic vestment, until it became arrayed in the glorious garb of the Human form.

Richard Owen, *On the Nature of Limbs* (1849), last paragraph.

9.1 The Tetrapod Limb

One of the classic evolutionary novelties is the tetrapod limb. Providing an adaptive framework to account for its basic nature and origin poses massive problems, as was already clear more than 160 years ago in Owen's classic work *On the Nature of Limbs*.¹ As we saw in Chapter 4, Owen argued in effect that the underlying *Bauplan* of the limb was an abstract, a-functional ground plan that had never served a specific function in any actual organism in any actual environment. This view—if true, and if it also applies to many other homologs—would upend completely the whole Darwinian paradigm.

As Owen showed, the adult functional forms of vertebrate limbs, including the forms of the digits, differ in extraordinary ways in different species; yet all are based on an unchanging underlying pattern or *Bau-plan*, the pentadactyl limb—“the one, two, five pattern.”²

Moreover, the forms of the fore and hind limbs are not identical in any known tetrapod species. Similarly, in no known tetrapod species is the morphology of all ten digits identical. This is obvious in the human body, where the bones of the leg and arm such as the femur and humerus are quite different, and the shapes of all ten digits differ from one another. The thumb and big toe, digit one, are very different from the other digits, made up of only two phalanges (a trait shared by all amniotes³), whereas all the other digits are made up of three. Although the other digits—two, three, four, and five—are fairly similar, they do differ in fine details: In the foot, each is successively smaller, while in the hand, the middle finger (digit three) is the longest; digit four is slightly longer than digit two in males; and the fifth digit considerably shorter than the other digits.

It is not just the skeletal structure of the limb *Bauplan* which is the same in hand and foot. As every medic learns in the dissection room, virtually every muscle in the hand has its homolog in the foot, as do the various ligaments and manner of attachment of the muscles and ligaments to the skeletal elements. The pattern of ossification of the metacarpals and metatarsals and phalanges is also the same in both the hand and foot. These profound homologies are obvious upon consulting any anatomy text. Although there are a few small differences in the muscles between hand and foot, the conservation of the same pattern is simply stunning given the completely different functions of the two organs, the foot for bipedalism and the hand for manipulation.

As we have seen, Owen's view was that the tetrapod limb *Bauplan*—a “primal pattern” as he termed it—could not be explained in terms of functionalism. Ironically, Darwin accepted Owen's interpretation in the case of the limb (and by implication in the

case of many of the other deep homologies), conceding that no adaptive explanation for the underlying *Bauplan* could be given. (See discussion in Chapter 4 above.)

Here I show that the origin of this major novelty, despite the great number of early amphibian fossils and putative amphibian ancestors which have been discovered since 1985, and despite huge advances in understanding the developmental genetics of the limb, is no closer today to any functionalist resolution than it was in Owen's day.

a. The Evidence from Fossils

When I wrote *Evolution*, I claimed: "It is generally presumed that the first amphibians evolved from fish and even the order of fish, the Rhipidistia, has been specified. However, transitional forms are lacking."⁴ The first amphibians, I claimed, had well-developed fore and hind limbs of normal tetrapod type. I conceded that fossil lobe-finned fish—which are closely related to amphibians found in the late Devonian alongside primitive amphibians—are the likely ancestors or close cousins of these early amphibians, but I claimed that the tetrapod limb did not arise through a long series of transitional forms subject to cumulative selection. Nearly thirty years on, the situation is exactly the same.

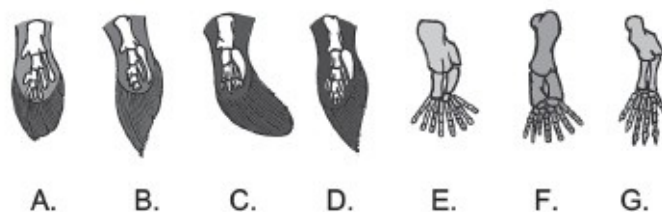


Figure 9-1. Fin to Limb Transition. The fins and limbs of several species close to the fin to limb transition. From left to right: *Eusthenopteron*, *Gorgonasmus*, *Panderichthys*, *Tiktaalik*, *Acanthostega*, *Ichthyostega*, and *Tulerpeton*.

In her book *Gaining Ground*,⁵ Jennifer Clack mentions a number of early amphibians found since *Evolution* was published: *Acanthostega*, *Tulerpeton*, *Ventostega*, and several more. Further, several fossil fish close to the fish-amphibian boundary, including the celebrated *Tiktaalik*, have also been found. But the gap between the tetrapod limb and the fin remains. As Clack commented on the recent discovery of *Tiktaalik*, much touted as a transitional form: "There remains a large morphological gap [see Figure 9-1 above] between them [the distal bones of the fin] and digits as seen in, for example, *Acanthostega*: if the digits evolved from these distal bones, the process must have involved considerable developmental repatterning."⁶ Moreover, the recent discovery in Poland of very obvious tetrapod tracks with developed digits, eighteen million years earlier than the previously earliest identified amphibian and ten million years earlier than the best transitional candidate (*Tiktaalik*),⁷ has complicated the issue further.

b. Evo-devo and the Origin of the Autopod

Although no one doubts that the tetrapod limb was assembled using pre-existing toolkit genes and gene circuits, these have been put together in unique ways to generate the tetrapod limb and the autopod (the third most distal part of the limb; the hand and wrist and foot and ankle). Günter Wagner concludes from an assessment of the latest evo-devo evidence that the autopod is what he terms a Type I novelty, a novel homolog without any antecedent in any fish fin.⁸ Others concur. In one of the most recent papers analyzing the developmental genetic differences between fin and limb, the authors conclude:

“[A]lthough fish have the Hox regulatory toolkit to produce digits, this potential is not utilized as it is in tetrapods, and as a result we propose that fin radials—the bony elements of fins—are not homologous to tetrapod digits.”⁹

That the digits of *Acanthostega* and other early tetrapods are novel homologs (shared by all subsequent tetrapod digits), and not proto- or pseudo-digits transitional between fish radials and true digits, is supported by recent work showing that the relative size of the phalanges in digits of all terrestrial vertebrates (tetrapods)—including, it would appear, in the very earliest amphibians—is determined by a special phalangeal developmental module (PDM) which regulates relative phalangeal size.¹⁰ The authors of a 2013 paper comment:

Successive phalanges within a digit exhibit predictable relative proportions, whether those phalanges are nearly equal in size or exhibit a more striking gradient in size from large to small... We find that phalangeal variation seen in nature is indeed constrained by an ancestral developmental program, limiting morphologies to a continuum from nearly equal-sized phalanges to a large-to-small gradient of relative sizes.¹¹

In the same paper, the authors showed by experimental perturbation of phalangeal development that each phalanx negatively influences the size of the next (proximal to distal), to an extent characteristic of each digit. They also showed that the metapodials (the metacarpals in the hand and the metatarsals in the foot) do not appear to influence phalangeal segmentation and accordingly appear to be generated by a distinct developmental module different from that which generates the phalanges. These results imply that the developmental module that constrains successive phalangeal size is homologous in all vertebrate limbs:

Measurements of phalanges across species from six major taxonomic lineages showed that the same predictable range of variants is conserved across vast taxonomic diversity and evolutionary time, *starting with the very origins of tetrapods*.¹²

So the evidence is at least consistent with the conception that the phalanges and metapodials have been determined by two distinct, novel, Type-defining developmental modules—a phalangeal developmental module (PDM) and a metapodial developmental module (MDM)—from the “beginning.” These two homologs—without any antecedent in fish fins—are two of the basic homologs that are combined to generate the unique form of the tetrapod autopod.

In a recent paper in *Science*, the authors showed that a Turing reaction-diffusion mechanism—such mechanisms are used commonly in biological systems where there is a reiteration of similar structures—is responsible for the spacing of the digits across the developing auto-pod and consequently for their number (what might be thought of as another developmental module—digit spacing and number module, DSM).¹³ These authors further showed that the Turing mechanism can be genetically re-engineered to change digit spacing and number. The authors also demonstrated that the segmentation of the digits into phalanges, governed by the PDM referred to above, could be altered or even abolished by genetically engineered changes in the same gene circuits involved in

establishing the Turing reaction-diffusion system. Moreover, the authors suggested that the Turing system far preceded the actualization of the autopod, and that its actualization involved novel utilization of existing gene circuits:

The emerging consensus suggests that the genetic toolkit patterning fins and limbs is largely conserved, and the evolution of digits was driven by accumulated regulatory changes controlling the spatial and temporal deployment of that common toolkit... The reduction of the distal *Hox* gene number in the absence of *Gli3*, which renders Shh signaling irrelevant, resulted in mouse digits losing defining characteristics (pentadactyl constraint and segmented morphologies) and exhibiting patterns reminiscent of the endoskeleton patterns in chondrichthyan and basal actinopterygian fins (numerous, iterative, densely packed, infrequently segmented elements). Thus, our data provide evidence that an ancestral Turing-like mechanism patterning fins has been conserved in tetrapods and modified by the implementation of regulatory changes in the evolution of digits.¹⁴

Other workers have confirmed that the same Turing reaction mechanism long predated the origin of the digits and autopod.¹⁵

Because this work implies that the developmental module determining phalangeal segmentation involves some of the same genes and gene circuits in extant tetrapod embryos as those involved in specifying the spacing of the digits across the autopod,¹⁶ it is possible that this was also the case in the very first tetrapods.

The evidence presented in these two papers suggests that the auto-pod actualized in the earliest tetrapods is a genuine, novel homolog possessed by all subsequent terrestrial vertebrates, which has remained basically unchanged for 400 million years. The evidence is consistent with the possibility that the three developmental modules responsible for generating the phalanges (PDM), the metapodials (MDM), and digit spacing and number (DSM) in extant limb development were present together in an integrated homolog in the very first tetrapod limbs. In short, there is no fossil evidence or evo-devo evidence that these homologs are not genuine novelties. Nor is there the slightest evidence of any gradual progression from proto-digits to true digits as was depicted in some earlier works.¹⁷ Whether these homologs that pattern the autopod originated first in one limb and were then redeployed to other limbs is not known, but it is assumed universally that the similarity is because of redeployment.¹⁸

As mentioned above, the morphology of the digits is not identical in any known tetrapod species, even if the differences in some cases are very slight. This implies that, although the basic design of all tetrapod digits is constrained by the same developmental module or *Bauplan*, the PDM,¹⁹ digit identity has been superimposed on top of this homologous pattern to allow different digits to acquire different adaptive designs (as in the bat's wing, etc.). This implies that actualization of the autopod involved yet another novel developmental module (digit identity module, DIM) to impose different identities on the individual digits. (Note however that the developmental genetics of digit individualization is complex, and complicated further by the existence of clade-specific digit identities.²⁰)

In many extant species, digit identity is established in the intervening tissues between

each digit as the digits themselves first form.²¹ However, the mechanisms involved are only partly understood.²² Whatever the mechanisms involved, since digit morphologies differ in some of the earliest tetrapods (see Figure 9-1), it must be presumed that digit identity was also acquired very early. If so, this would mean that the earliest autopods differed from extant autopods only by the absence of one additional developmental constraint: pentadactyly. All other novel developmental modules operating in extant limbs may have been already operational in the very first tetrapods. At the least, the evidence (evo-devo and fossil) is consistent with such a view.

The final step towards the “modern autopod” was the imposition of the constraint of pentadactyly. The very earliest autopods were not subject to this constraint, possessing six, seven, or eight digits (see Figure 9-1); however, pentadactyly is the norm for all post-Devonian tetrapods—all subsequent amphibia, reptiles, mammals, and birds—and can be considered as another Type-defining novelty or homolog. Wagner uses the term “Pentadactyl Autopodium Type”²³ to distinguish the clade of post-Devonian pentadactyl tetrapods from the earlier Devonian polydactylous tetrapods.²⁴ Although there are fundamental differences in the processes underlying autopod development in post-Devonian tetrapods—salamanders, frogs, and amniotes²⁵—none have more than five true digits.²⁶

Thus, it seems that the actualization of the tetrapod limb must have involved at least two successive steps: (1) the origin of the autopod itself; (2) the subsequent imposition of pentadactyly. As to the first step, the evidence (fossil and evo-devo) suggests that the novel homologs (Owen’s atomic building blocks), which together constitute the basic autopod, may have been acquired *per saltum*. One additional line of evidence that supports this conjecture is that the fin rays would have to have been lost before the autopod replaced them.²⁷ As it is somewhat difficult to envisage a fish without fin rays being advantaged in any way, the idea that the conversion was sudden seems at least plausible.

If the novel developmental homologs (PDM, MDM, DSM, DIM, etc.) involved in making the limb were in fact acquired together *per saltum*, the acquisition would be absolutely inexplicable in any sort of Darwinian framework. Nothing nearly as complex as the limb or auto-pod could possibly have come about *per saltum* without underlying direction. To ensure the orderly and coordinated growth of an organ like a hand—comparable in terms of complexity with a whole embryo—the timing and positioning of the expression of all the genes involved must be rigidly controlled, as must the regulation of the growth and development of all the constituent tissues. Cartilage formation, novel patterns of tissue growth, cell migration and apoptosis, nerve and muscle cell formation, all must be tightly regulated. Sean Carroll comments: “It appears that this new structure [the autopod] has evolved because a set of vertebrate *Hox* genes have acquired a new switch or set of switches that activate them in a new distal part of the embryonic limb.”²⁸ But the overall process must have involved far more than a few genetic switches. Carroll continues:

These were not the sole changes involved. There were many other developmental changes and genes involved in shaping of the autopod. Other genes, such as members of the bone-promoting *BMP* family and the joint-making *GDF* family, acquired digit-specific switches, and all of the soft tissues

—tendons, ligaments, and muscles—and the genes that control their formation and patterning evolved as well.²⁹

No matter what Darwinian evolutionary “spin” is put on the gap between fin and hand, there is no avoiding the fact that a significant break does exist in the natural order, and the new evo-devo picture provides no support for any sort of Darwinian gradualist, functionalist scenario. Moreover, irrespective of the empirical evidence, fossil and evo-devo, which suggests that the limb homolog was put together in either a series of leaps, or a single major leap, trying to envisage the process as occurring under the direction of gradual natural selection poses herculean challenges.

In sum, it is now clear from advances in evo-devo that the tetrapod limb is not just one unitary homolog, but a combination of homologs. The tetrapod limb is built like the animal body from a combination of Owen’s atoms—the phalangeal developmental homolog or module (PDM), the metapodial homolog (MDM), the digit spacing module (DSM), the digit identity module (DIM), the “pentadactyl developmental homolog,” and so forth. The formula of the limb, following Owen’s atomic conception of the organism as a combination of basic homologs, would be: PDM + MDM + DSM + DIM +... The tetrapod limb is not, then, an individual “primal pattern” in Owen’s terms, but a composite of several “primal patterns,” and each is the result of a highly integrated, novel set of developmental processes.

c. Just-so Stories

Given the facts just described, attempts to explain how the tetrapod limb developed through a Darwinian process quickly devolve into “just-so stories.”

Consider first the difficulties that are immediately encountered in trying to account for digit number in terms of pure adaptationism. The number of digits in the earliest tetrapods was variable: Some tetrapods had eight digits, others seven, others six. Immediately questions arise. What adaptive purpose did the eight digits serve in *Acanthostega*? What adaptive purpose did seven serve in *Tulerpeton*? What functional constraints called for the specific number of digits in these species? And what was so magical about the number five, which led to its fixation as the canonical digit number in all subsequent post-Devonian tetrapods. Why not six? Surely causal factors other than selection were involved in all cases. Perhaps pentadactyly arose from pre-existing genetic architecture, which channeled the development of the limb toward the five-digit design. In any case, whatever the answer it is hard to believe that cumulative selection was the main causal agency.

Accounting for the magical significance of the number five is a trivial problem compared with the nightmare of trying to provide an adaptive explanation for the shared ground plan of the ten digits in all tetrapods and the fact that they are all generated by the same homologous developmental module (PDM).³⁰

Just as the fore and hind limbs always differ in all adult tetrapods, so do the digits in both the hand and foot, sometimes very dramatically. In no known species are *all* the digits identical in either the hand or the foot—even in species where the differences are very slight.³¹ In winged reptiles (pterosaurs), the wing is supported by a massively enlarged fourth digit. In bats, the wing is supported by massive enlargement of digits two, three,

four, and five, while digit one is “normal-sized.” In the horse, digit three is massively enlarged while the other digits are massively reduced.³² Further, in human beings, the thumb (digit one) and the big toe in the foot (digit one) have two phalanges, while the other digits always have three. Again, as mentioned above, the middle digit (three) of the human hand is longer than the other two adjacent digits (two and four), while in the foot the size of the digits decreases from the big toe (digit one) to the little toe (digit five), which is almost vestigial.

Self-evidently, no plausible functionalist explanation can be given to account for the shared ground plan of all ten digits and the fact that the ontogeny of all ten digits is constrained by the same underlying PDM. Given their variable morphologies in adult tetrapods, the suggestion that cumulative selection put together this unique developmental module in one digit to serve some obscure functional reason, then assembled the same module independently in a second digit and so on for all five digits in the hand and the five digits in the foot in some ancestral form, is too bizarre to contemplate, leading only to “endless absurdities” as Bateson put it. Clearly, the digits are a case (like the fore and hind limbs) of serial homology where the same ground plan was adopted or redeployed in all digits, either at once or successively, for reasons that are obscure but certainly could hardly have anything to do with direct adaptation to serve some function in some particular environmental setting. Every aspect of digit origins bristles with seemingly intractable problems when an attempt is made to provide a Darwinian explanation. For example, by what curious adaptive path did the growth of the more proximal phalange come to restrain the size of the next most distal phalange? Again by what obtuse path arose the constraint which limits digit one (the thumb and big toe in man) in all amniotes to only two phalanges? It is, I submit, very difficult—indeed I would say impossible—to envisage these patterns as arising from functional constraints.

Explaining how all the digits came to have the same basic ground plan in adaptive terms is highly problematic, but equally problematic is how digit identity was first imposed by cumulative selection. The catch is this: Until digit identity is imposed, none of the digits can acquire a different morphology, yet digit identity only has adaptive utility when the digits exhibit a different morphology. This is another classic chicken-and-egg problem.

What applies to the ten digits also applies to the fore and hind limbs. Just as the digits are serially homologous, so are the fore and hind limbs. Yet in all adult terrestrial tetrapods, when the limbs are actually used in the organism’s “day to day struggle to survive,” and hence under selectionist pressures, *the fore and hind limbs are never identical*.³³ This implies that utility demands a different form for fore and hind limbs; and common sense would suggest the same must surely have applied in the mysterious elusive ancestral tetrapods that according to Darwinism were gradually acquiring the forms of their limbs under the supervision of natural selection in the late Devonian swamps. It is hard to escape the logic here. There cannot have been two identical yet separate functional continuums leading to fore and hind limbs. Of course no one accepts that scenario. It is generally agreed that the pattern was acquired in one of the limbs (fore or hind) and then redeployed to the other limb (fore to hind or hind to fore). But this implies *that structural internal factors, i.e., factors other than selection for direct biological utility, must have been involved in imposing the same design on both fore and hind limbs*.

Recent studies have shown, not surprisingly, that some of the basic developmental processes that generate the fore and hind limbs in tetra-pods are also used to generate the pectoral and pelvic fins in fish and that therefore the lateral appendages are homologous throughout the vertebrate series.³⁴ Assuming, for the sake of argument, the developmental program in tetrapods was inherited from fish ancestors, we are still faced with the difficulty of explaining how the same ground plan arose in the pectoral and pelvic fins. For one thing, in no known adult fish (including the lobe-finned fishes from which amphibians or tetrapods are derived) is the form of the pectoral and pelvic appendage identical.³⁵ So we meet the same problem: how could selection for function have led to the same ground plan for pectoral and pelvic fins in fish?

Finally, Wagner notes a further intriguing observation which militates against the notion that the unique design of the tetrapod limb can be explained in terms of functional need. As he points out: “Even the most terrestrial teleosts (Periophthalmus, mudskippers, some blennies, eels and tropical catfish) do not acquire anything remotely similar to a tetrapod limb.”³⁶

I have so far argued that no Darwinian account of the origin of this defining homolog (or of its various constitutive homologs) can be given. But there is a potentially greater problem for Darwinism: The imposition of the same ground plan on fore and hind limb may not only be of dubious adaptive utility, *but actually maladaptive*. Owen hints darkly at this in *On the Nature of Limbs*. Given that fore and hind limb difference is the adaptive state for terrestrial vertebrates, the redeployment of the pentadactyl pattern from fore to hind or hind to fore must be viewed “formally” as maladaptive.

Summary

Since I wrote *Evolution: A Theory in Crisis*, no forms illustrating a genuinely transitional state between a fin and limb have come to light. Further, nothing gained through the extensive genetic and developmental studies of limbs provides any support for the notion that the autopod was acquired gradually via a vast number of tiny microevolutionary adaptive steps over hundreds of thousands of generations. It is true that the auto-pod is composed of a combination of separate developmental modules or “primal patterns,” but each of these may be considered a Type-defining novelty or homolog in its own right, none of which is led up to either empirically or hypothetically via Galápagos-type gradual transitional forms. Moreover, saltational modes of origin would seem unavoidable, as the only way the homology of the ten digits can be explained is by saltational redeployment of an identical developmental module. The fact that no Devonian vertebrate has been found with a partly evolved auto-pod (with fin rays and digits) and that none has been found with a pectoral fin and a tetrapod hind limb, point, in conjunction with the developmental evidence, to the origin of the limb as a saltational event. Apart from the developmental constraint of pentadactyly, perhaps the entire suite of developmental mechanisms involved in making the hand and foot were present in the very earliest tetrapods. As things stand, I believe that the evidence supports the structuralist interpretation of the origin of the tetrapod limb—i.e., that it represents a robust emergent natural form or composite form which was actualized relatively suddenly at a particular moment in vertebrate evolution as a result of internal causal factors rather than by cumulative selection to serve functional ends.

Owen saw the limb *Bauplan* as an abstract form that transcended any functional particular. Nothing discovered in the past 160 years invalidates his view.

9.2 The Feather

One of the adaptive wonders of nature is the wing of the bird. In *The World of Life*, Alfred Russel Wallace praised it as follows:

Looking at it as a whole, the bird's wing seems to me to be, of all the mere mechanical organs of any living thing, that which most clearly implies the working out of a preconceived design in a new and apparently most complex and difficult manner, yet so as to produce a marvellously successful result.³⁷

Wallace realized that in the design of the bird's wing the crucial element was the feather:

The idea worked out was to reduce the jointed bony framework of the wings to a compact minimum of size and maximum of strength in proportion to the muscular power employed; to enlarge the breastbone so as to give room for greatly increased power of pectoral muscles; and to construct that part of the wing used in flight in such a manner as to combine great strength with extreme lightness and the most perfect flexibility. In order to produce this more perfect instrument for flight the plan of a continuous membrane, as in the flying reptiles (whose origin was probably contemporaneous with that of the earliest birds) and flying mammals, to be developed at a much later period, was rejected, and its place was taken by a series of broad overlapping oars or vanes, formed by a central rib of extreme strength, elasticity, and lightness, with a web on each side made up of myriads of parts or outgrowths so wonderfully attached and interlocked as to form a self-supporting, highly elastic structure of almost inconceivable delicacy, very easily pierced or ruptured by the impact of solid substances, yet able to sustain almost any amount of air-pressure without injury.³⁸

The origin of the feather is as puzzling as the origin of the tetrapod limb or the enucleate red cell. To be sure, unlike the enucleate red cell or the “primal pattern” of the tetrapod limb, the feather is clearly an adaptive form, useful for flight, for insulation, for sexual display, etc. Further, no one doubts the utility of the stages that led from the simple follicle through the plumaceous feather to the closed pennaceous contour feathers of modern birds (see Figure 9-2). Yet this taxon-defining novelty appears to be just as inexplicable in Darwinian terms. Cumulative selection cannot even begin to account for the origin of the series of novelties that make up the avian feather.

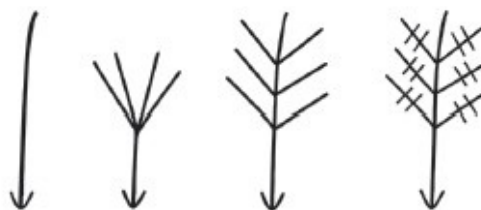


Figure 9-2. Novelties in Feather Evolution. From left to right: (1) the feather follicle and first feather consisting of single cylindrical filament; (2) the plumaceous feather with parallel unbranched barbs; (3) the bipinnate feather with unbranched barbs attached to the rachis; and (4) the open pennaceous feather with branched barbs (i.e., barbs with

barbules). The next stage is not shown: the development of the closed pennaceous feather resulting when the barbules in (4) acquired interlocking hooks (the barbules pointing to the feather tip) and grooves (the barbules pointing to the feather base), which bound the barbs together into the closed vane shown in Figure 3-3.

When I wrote *Evolution: A Theory in Crisis*, the evolution of the feather was dominated by the “frayed reptile scale” paradigm. I quoted Gerhard Heilmann: “By the friction of the air, the outer edges of the scales become frayed, the frayings gradually changing into still longer horny processes, which in course of time become more and more feather-like, until the perfect feather is produced.”³⁹

Heilmann also claimed (wrongly as we now know): “In their development the feather and the scale are exactly alike, the feather being a cylindrical fringed scale.”⁴⁰

More recently, Regal has defended the frayed-scale model, providing the following diagram:⁴¹



Figure 9-3. Frayed-Scale Model. Hypothetical intermediate stage in the evolution of feathers from scales showing “cracks” separating sections of a large scale into smaller, lateral plates, or protobarbs. [Reproduced with permission of University of Chicago Press via Copyright Clearance Center.]

Such models have the “Darwinian merit” of building a novel form bit by bit through cumulative selection. Darwin, Mayr, and Dawkins would have approved! My judgment of the hypothesis was expressed with a quotation from Barbara Stahl’s lucid *Vertebrate History: Problems in Evolution*: “How they arose initially... defies analysis.”⁴² The truth of her comment is now apparent from the recent revolution in our understanding of feather origins, which implies that feathers are an evolutionary novelty and were not derived from reptile scales.⁴³

The deconstruction of the classic “frayed-scale” model was the work of a few insightful scholars, the most prominent being Richard Prum, currently at Yale.⁴⁴ In a landmark article in the *Quarterly Review of Biology*, Prum and Alan Brush comment:

Over the last half of the 20th century, neo-Darwinian approaches to the origin of feathers, exemplified by Bock (1965), have hypothesized a microevolutionary and functional continuum between feathers and a hypothesized antecedent structure (usually an elongate scale). Feathers, however, are hierarchically complex assemblages of numerous evolutionary novelties—the feather follicle, tubular feather germ, feather branched structure, interacting differentiated barbules—that have no homolog in any antecedent structures.⁴⁵

Although the origin of the feather occurred via a succession of novelties (see Figure 9-2), the new evo-devo picture provides not the slightest evidence that any of the novelties leading to the feather were actualized by cumulative selection. As Prum and Brush comment: “Although evolutionary theory provides a robust explanation for the appearance of minor variations in the size and shape of creatures and their component parts, it does not yet give as much guidance for understanding the emergence of entirely new structures, including digits, limbs, eyes and feathers.”⁴⁶

As they show from recent work on the feather, it is clear that, again, many of the genes and developmental systems utilized in feather morphogenesis pre-existed the origin of the feather, including the pattern-forming genes sonic hedgehog (*Shh*) and bone-morphogenetic protein2 (*Bmp2*), which are utilized widely in the development of hair, limbs, digits, teeth, and the Turing reaction-diffusion mechanism.⁴⁷ These are all components of the universal toolbox. During feather development, the two toolkit proteins *Shh* and *Bmp2* “work as a modular pair... The *Shh* protein induces cell proliferation and the *Bmp2* protein regulates the extent of proliferation and fosters cell differentiation.”⁴⁸ These two proteins are used repeatedly throughout feather development from the initial formation of the placode to the later laying down of the pattern for the helical growth of the barb ridges.⁴⁹ But despite the co-option of pre-existing gene circuits, all the evidence points to feathers being genuine novelties, not homologous to reptile scales or any known antecedent structure.⁵⁰

a. The Follicle

The first key innovation in the evolution of the feather was the feather follicle. This first novelty is without any antecedent structure in any reptile scale or any other vertebrate skin appendage. It is a unique epidermal invagination that leads to the growth of a hollow tube—a tube that Prum calls “the defining feature of the feather.” Without this primal innovation, there would be no subsequent development of barbs, no helical growth pattern generating the rachis, and no closed pennaceous feather. The tubular nature of the feather is therefore the primary novelty upon which all the subsequent innovations leading to the modern pennaceous feather are built.⁵¹

Prum commented to Thor Hanson, “Without the [tubular] follicle, a feather would basically be like a wart.”⁵² And in response to Hanson’s question, “[W]hen do you call a feather a feather?” Prum replied: “If it’s a hollow tube, it’s a feather... One thing I keep saying again and again is that there is no such thing as a ‘protofeather.’ No one talks about a ‘protolimb.’ You either have a limb or you don’t. Why should feathers be any different? If it’s a tube, it’s a feather. Period.”⁵³

Prum’s recognition of the *fundamental tubular nature of feathers* came to him in a moment of epiphany while lecturing students on the old frayed-scale-to-feather theory.⁵⁴ Suddenly he recognized a very fundamental difference in the way scales and feathers grow.⁵⁵ In Hanson’s words:

There is a fundamental structural difference between scales and feathers and how they grow. Scales form like plates, flat ridges protruding outwards as extensions of the epidermis. It’s like the contrast between a napkin and a straw. Fold the napkin and you have a scale, with the outer surface—the epidermis—covering both top and bottom... [But in the case of feathers they]... flatten by *opening up*. The outer surface becomes the top and the inside is revealed to become the bottom. So while a mature feather and a scale may both appear flat, their surfaces simply don’t correspond.⁵⁶



Figure 9-4. Pennaceous Feather. The helical pattern of growth of the pennaceous feather. “The branched structure of the barbs and the rachis of a feather form by helical growth and fusion of barb ridges within the tubular feather germ. Feathers grow from the base. Barb ridges form at the new barb locus on the posterior midline of the collar and grow helically around the collar toward the anterior midline where they fuse to form the rachis ridge. Subsequent barb ridges fuse to the rachis ridge. In feathers with an after-feather, the new barb locus divides into two laterally displaced new barb loci.” [R. O. Prum, “Development and Evolutionary Origin of Feathers,” *The Journal of Experimental Zoology* 285, no. 4 (December 15, 1999): 294.]

Moreover, the initial stages of follicle formation, the formation of the placode, involves a proliferation of epidermal cells above a condensation of dermal cells, which is also a definite novelty. As Prum and Brush point out: “Avian reticulate scales... and all reptilian scales examined to date lack a morphologically definable placode.”⁵⁷ Neither Prum nor any other author to my knowledge has provided a Darwinian scenario in which an adaptive continuum leads from the placode to the actualization of the feather follicle.

b. Subsequent Novelties

Following the establishment of the follicle (Figure 9-2, first image), the mature feather results from a succession of fascinating novel developmental mechanisms, which have, as mentioned above, no homolog in any reptilian scale or indeed any vertebrate integumental structure.

As described by Prum and Brush,⁵⁸ these include (Figure 9-2) the development of parallel barb ridges in the follicular collar leading to the simple unbranched plumaceous feather. (For further clarification see a video posted on the web.⁵⁹) The next stage (see Figure 9-2, third image, and aforementioned video⁶⁰), involves the helical growth of the barb ridges from the anterior to posterior and their fusing together to form the rachis and the bipinnate feather. The next stage (see Figure 9-2, fourth image) involves the formation of barbules—distal pointing towards the tip of the feather and proximal pointing towards the base, forming a bipinnate open pennaceous structure. Finally there is the development of hooks on the distal barbules and interlocking grooves on the proximal barbules which hold the barbs together into the closed pennaceous vane of the common contour feather.⁶¹

As mentioned above, it is not just the feather follicle that is without any antecedent; so are the other successive novelties described above. In Prum and Brush’s words:

Müller and Wagner defined a morphological novelty as a structure that is neither homologous to any ancestral structure nor homonomous (i.e., serially homologous) with any other structure in that organism. Many features of feathers and feather helical development meet this definition and qualify as evolutionary novelties. The *follicle*, the *differentiated sheath and feather germ*, *differentiated barb ridges*, *barb rami*, *barbules*, *differentiated pennulae* of the proximal and distal barbules, and the *rachis* are all evolutionary novelties.⁶²

Of course, it is not only the visible macroscopic morphological novelties that are without antecedent but also the underlying “invisible” network of generative

developmental mechanisms involved in their actualization.⁶³

This is not the place for a detailed description of every aspect of feather development, but one stage, the helical displacement of the developing barb ridges to meet the rachis, is a truly remarkable phenomenon. Viewing the video simulations conveys graphically the full enormity of the challenge to Darwinian cumulative selection implicit in feather development. Perhaps there was a functional intermediate between the parallel barbs of the plumaceous feather and the branched barbs of the open pennaceous feather, but one can only echo what Gould has said in so many other instances: What these functional transitional forms were is very difficult to envisage. The problem here is like that of the enucleation of the red cell: The key developmental changes which lead to a helical pattern of barb growth must be in place or emerge before the barbs can be attached to the rachis. What adaptive utility resided in the underlying developmental changes that led to the helical twist and the feather with branched barbs? The evidence is certainly compatible with the notion that the helical twist was acquired *per saltum*. And not just the helical twist. The fact that all the above stages are quite distinct, and that there is an empirical gap between each stage—that no known feather structures bridge the stages in either living or fossil species—is highly suggestive.

The jump between the parallel barbs of the plumaceous feather and the helically twisted barbs in the pennaceous feather is complex. It has been recently shown that the parallel barbs are generated by a two-component activation-inhibition mechanism (Turing-type reaction-diffusion mechanism), while the helical twist and the joining of the barbs to the anterior rachis involves an additional component, making up a three-component Turing-type reaction. Clearly a great many other, yet-to-be-identified changes must also be in place to cause the helical displacement toward the anterior of the feather.⁶⁴ These are bound to include a number of additional novel gene expression patterns in addition to those associated with setting up and regulating the two different Turing mechanisms. Some indication of the complexity of these additional factors is conveyed in a *Nature* paper describing some of the genes expressed in the developing feather.⁶⁵ The authors comment:

We show that the antagonistic balance between noggin and bone morphogenetic protein 4 (BMP4) has a critical role in feather branching, with BMP4 promoting rachis formation and barb fusion, and noggin enhancing rachis and barb branching. Furthermore, we show that sonic hedgehog (SHH) is essential for inducing apoptosis of the marginal plate epithelia, which results in spaces between barbs. Our analyses identify the molecular pathways underlying the topological transformation of feathers from cylindrical epithelia to the hierarchical branched structures, and provide insights on the possible developmental mechanisms in the evolution of feather forms.⁶⁶

Every aspect of feather origins bristles with challenges to Darwinian scenarios. To take a minor example, without apoptosis of the cells between the barbs and barbules (as in the developing digits in the auto-pod) neither barbs or barbules could exist as separate filamentous structures. What came first, the cellular condensation, that created the barbs (which occurs first in the development of extant feathers), or the apoptosis (which occurs after the development of the barbs in extant feathers) that separated them into discrete

filaments? Only if both developmental processes are in place can the adaptive end of a branched feather be actualized, which again raises the specter of evolution *per saltum*. Again, severe problems arise in trying to imagine a Darwinian scenario for the origin of the barbules and their subsequent differentiation into distal barbules with hooks and proximal barbules with grooves, which inter-lock together, binding the pennaceous feather into a closed vane. In attempting to reduce feather origins to Darwinian scenarios, we are led not only into “endless absurdity,” but into direct conflict with what is known of the developmental processes underlying the ontogeny of the feather. There is no sanction in the developmental processes underlying feather ontogeny for one-by-one, bit-by-bit Darwinian functionalist approaches.

Finally, just as digits have individual identities, so feathers also have individual identities; this is obvious on cursory examination of any bird. Some feathers are plumaceous, some are closed pennaceous vanes, etc. And not only are feathers individualized but regions of feathers also. This can be seen in the different patterns painted on individual feathers, as in the eyes on the display feathers of a peacock.



Figure 9-5. Peacock feathers.

Again, as with digit identity, what came first, individualization or the imposed adaptive pattern? How can a genetic program “see” a region of a particular feather until feathers and their “parts” have been genetically and developmentally differentiated? What utility is individualization, especially of *different regions of feathers*, until it is put to adaptive use? The complexity of the underlying development processes which lead to the thousands of individualized feathers and feather regions of a peacock beggars belief! And again, as in the case of digits, the individuation of one feather logically implies the simultaneous individuation of others. This is another pointer to saltational change.⁶⁷

Summary

The origin of the various feather novelties and the developmental processes that actualize them are enigmatic in classic Darwinian terms. Prum and Brush conclude:

By emphasizing the reconstruction of a series of functionally and microevolutionarily plausible intermediate transitional states, neo-Darwinian approaches to the origin of feathers have failed to appropriately recognize the novel features of feather development and morphology, and have thus failed to adequately explain their origins.⁶⁸

Evo-devo research on the feather has finally laid to rest the Darwinian “frayed reptile scale” scenario. Feathers and scales are fundamentally different skin appendages. As Thor Hanson comments: “What Prum recognized now seems obvious: there is a fundamental

structural difference between scales and feathers and how they grow.”⁶⁹ Although it is clear that the feather was actualized in stages, which can be followed in the fossil record,⁷⁰ there are no known adaptive sequences leading gradually to each of the novelties or new homologs.

On any common-sense assessment of the evidence now available, it would seem that the feather arose (like the limb *Bauplan*) because of internal causal factors and not to serve functional constraints. In this regard, it is intriguing that Matthew Harris et al. comment in their *PNAS* paper: “The signaling mechanisms that produce complex barb branching in pennaceous feathers were an *inherent potential of the molecular mechanisms previously evolved* with the origin of simpler, plumulaceous feathers.”⁷¹ The current picture of feather origins is perfectly consistent with a typological/structuralist interpretation: that the succession of novelties represent a series of in-built robust natural emergents or natural forms, each arising successively but inevitably from the inherent properties of the follicle actualized during the immediately preceding evolutionary stage. In terms of typology, one can view each novelty as a Type-defining homolog, defining a series of increasingly exclusive Types along the lineage leading to modern birds.

Alfred Russel Wallace eulogized the adaptive wonder that is the feather in *The World of Life* and saw its intricate design as evidence of an “organizing and directive life principle.”⁷² Nothing that is currently known about feather development invalidates Wallace’s inference.

9.3 How the Bat Got Its Wings

Another classic taxon-defining novelty is the wing of the bat. The traditional Darwinian view explains the origin of this novelty by positing the adaptive utility of intermediate forms with partly developed wings. In *Evolution: A Theory in Crisis*, I quoted Glenn Jepson’s rebuttal of this view: “No one has successfully proposed any kind of selection pressure that would be effective in the change from one niche to the other; whether the bridging group would be pulled by advantages in the new milieu or pushed by disadvantages to the old.”⁷³ As to the likelihood of going from a “gliding wing” to a wing capable of powered flight, Jepson further remarked:

Morphologically and genetically and phylogenetically the distance from a gliding habit to a bat-flying habit among known mammals is so immense that a development of the former may almost be said to preclude the probability of further development in the same phyletic line to the latter.⁷⁴

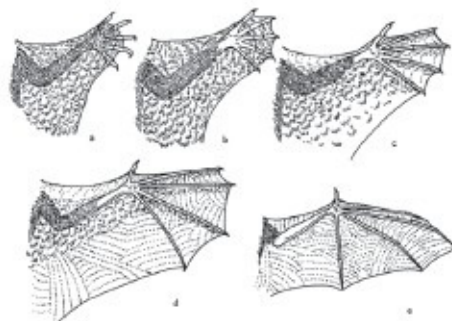


Figure 9-6. Bat Wing Evolution. Hypothetical progressive stages in the development of the bat’s wing. [Reproduced with permission of Plenum Press via Copyright Clearance Center.]

In *Evolution*, I also alluded to the absence of any intermediate forms in the fossil record: The earliest known bat had wings as developed as those of modern forms and was as completely adapted for powered flight as a modern bat. Thirty years on, this is still the case.⁷⁵ The authors of one recent paper comment: “The earliest known bats appear in the fossil record... [about] 50 million years ago, and they appear suddenly and already possessing the anatomical hallmarks of powered flight.”⁷⁶ They go on to say that the evidence suggests “that bats achieved powered flight in a few million years, which is a relatively short span of geologic time.”⁷⁷

Like the feather (but unlike the ground plans of the tetrapod limb and the angiosperm flower and many other *Bauplans*) the hand-wing of the bat—a common design shared by all bat species—is obviously an adaptive structure. Yet it remains difficult to envisage how it might have been actualized via a Darwinian functional continuum.

Currently there are sixty-four different mammalian species capable of gliding flight, possessing a flap of skin extending from fore to hind limb—a patagium.⁷⁸ These include the flying (more properly gliding) squirrels,⁷⁹ flying possums, a group of central Asian flying rodents belonging to a clade separate from the flying squirrels,⁸⁰ and the colugo.⁸¹ An extinct placental gliding fossil mammal, *Volaticotherium antiquum*, is known from the Cretaceous as well.⁸² But *all* these species have or had functional “hands” only very slightly modified from the typical forelimb of a small arboreal mammal (see Figure 9-6, stage a). In addition to mammals, many other vertebrates “invented” gliding flight,⁸³ including more than 3,000 species of frogs.⁸⁴

The fact that there are so many gliding animals is not so surprising. It is very easy to envisage a Galápagos-type hypothetical functional “continuum” leading from a “mouse” to a small gliding rodent with slightly elongated fingers and retaining webbing between the digits, and even possessing a patagium. Given the selective advantage of jumping from tree to tree, avoiding ground predators, and saving energy to reach a new food source, all the while maintaining functional forelimbs, the development of gliding capacity is almost inevitable. But it is quite another matter to envisage a functional continuum (Figure 9-6, stages b through d) leading to the bat hand-wing (Figure 9-6, stage e). No forms are known which possess such “intermediate” wings (or gliding devices).⁸⁵

An interesting parallel is found in the case of another class of flying vertebrates with wings composed of extended membranes of skin—the pterosaurs. There are also no known intermediate fossils of pterosaurs. In his recent book, Mark Witton shows a drawing of a hypothetical proto-pterosaur, but concedes that the fossil record has yet to reveal an “intermediate” form between full-fledged pterosaurs and their possible ancestors.⁸⁶ Consequently, he cautions, “we can only speculate on their anatomy and appearance... Much of their anatomy is so significantly different from that of other reptiles that their specific evolutionary origins are obscured. In addition, we have yet to find any “protopterosaur” species that bridges the gap between them and their reptilian ancestors.”⁸⁷

The extraordinary inventory of changes in bat morphology which enabled powered flight was captured in one of the most recent reviews in this area:

Beyond the presence of wings, adaptations to powered flight encompass most

organ systems including: [1] full flexion and extension of whole wing (including hyper abduction of digits) automated via tendon rearrangements... [2] energy-saving locking mechanisms such as vertebral column rigidity... [3] locking mechanisms in each forelimb joint to prevent hyperextension or rotation of the wing... [4] concentration of forelimb muscle mass towards the center of gravity to reduce inertial power... [5] leading-edge camber adjustment by pronation of hand assisted by tension of propatagium via m. occipitopollicalis and stiffened dactylopatagium minus... [6] trailing-edge camber adjustment by flexion of digit V... [7] streamlining of the head–body to reduce parasitic drag, placing of the head in between scapular blades by dorsiflexion of neck... and rotation of basicranial axis with respect to rostrum... [8] rotation of hind limb segments by modification of hip and ankle joints to spread laterally and caudally... [9] tendon locking mechanism as energy-saving device used in hindlimb suspension... [10] synchronization of wingbeat and respiratory cycles... [11] mass specific aerobic capabilities and cardiac outputs at least twice as high as those of running mammals... [12] adaptive changes in genes involved in energy metabolism... [14] specialized capillary circulation in the wing membrane.⁸⁸

The reviewer goes on to comment: “many of these characters represent unreversed synapomorphies [or novelties] of Chiroptera,” and confesses (understandably, given this long list of unique adaptations) that “exactly how bats achieved the morpho-functional conditions of flight, and how the many refinements of wing morphology were attained, *remains poorly understood*.”⁸⁹

Given the great complexity of these morphological changes, one would imagine that the actualization of this novelty would require a host of complex integrated developmental changes involving a considerable number of gene circuits. Recent evo-devo studies have confirmed this, by revealing that indeed a great number of novel gene circuits and gene expression patterns accompany the development of the bat’s wing.⁹⁰ Regarding their recent study, which looked for genes differentially expressed in the developing bat wing, the authors comment:

Overall, comparisons of gene expression profiles [between short and long digits] ... identified *hundreds of differentially expressed genes*. Several interesting patterns have emerged from this data... we found 14 genes that are likely associated with digit elongation in bats—two *Tbx* genes (*Tbx3* and *Tbx15*), five genes from the BMP pathway (*Bmp3*, *Rgmb*, *Smad1*, *Smad4* and *Nog*), four Homeobox genes (*Hoxd8*, *Hoxd9*, *Satb1* and *Hoxa1*) and three other genes (*Twist1*, *Tmeff2* and *Enpp2*) related to either digit malformation or cell proliferation.⁹¹

As the study implies, the origin of the bat’s wing was much more complex than the mere evolution of a new enhancer [genetic switch]—such as may have played a significant role in the origin of some simpler novelties (see Carroll on the evolution of eye spots⁹²)—or the modulation of existing gene circuits which sculpted the beak shapes of the Galápagos finches. In a more recent paper summarizing their results, the same authors comment:

These results suggest multiple genetic changes occurred independently during

the evolution of bat wings to elongate the hand digits, promote membrane growth and keep other digits short. Our findings also indicate that the evolution of limb morphology depends on the complex integration of multiple gene regulatory networks and biological processes that control digit formation and identity, chondrogenesis, and interdigital regression or retention.⁹³

To date there is no evidence that these novel gene circuits and expression patterns were acquired successively, in conformity with Darwinian gradualism and its assumption that macroevolution is a mere extrapolation of microevolution.⁹⁴ Commenting on the likely underlying genetic complexity of the hand-to-wing transformation and the question whether microevolution can be extrapolated to macroevolution, Kimberly Cooper and Clifford Tabin remark:

It has long been debated whether the processes and mechanisms responsible for phenotypic variation within a population or between closely related populations can be extrapolated to explain... the generation of novel structures. Although there has been great progress in recent years in addressing the genetic basis for micro-evolutionary changes, for the most part these efforts have done little to address this debate... While it is still unclear whether modern bats arose rapidly or gradually from their quadrupedal ancestor, it does seem certain that their evolution required many molecular changes to dramatically alter morphology from a limb to a wing.⁹⁵

Some researchers have claimed that a “*simple* change in a *single* developmental pathway... [might lead to] dramatically different morphologies... [thus providing] a potential explanation as to how bats were able to achieve powered flight soon after they diverged from other mammals nearly 65 million years ago.”⁹⁶ In the light of the emerging developmental-genetic picture this view looks overly optimistic. Research such as Günter Wagner’s work on the origin of placentation (see Chapter 7 above) provides similar grounds for doubt, providing further evidence that the origin of evolutionary novelties (new homologs) like the bat’s wing may involve very complex re-wiring and recruitment of multiple gene circuits—perhaps even simultaneously.

Some insight into the very great developmental complexity of the transition and the need for integrated and new compensatory regulatory circuits is indicated by the fact that Bmp2 (bone morphogenetic protein 2), which promotes chondrocyte proliferation and maturation (cartilage formation) and digit elongation in the bat wing,⁹⁷ in ordinary non-volant mammals also causes apoptosis of the membrane (the web-bing) stretching between the digits in the embryo.⁹⁸ In bats the webbing is preserved because of the unique expression of two genes, *Gremlin* and *Fgf8*, in the interdigital regions, which represses bone-morphogenetic, protein-induced apoptosis.⁹⁹ In other words, only the recruitment and simultaneous activity of new compensatory gene circuits enabled bats to extend their digits while at the same time retaining the intervening webbing!

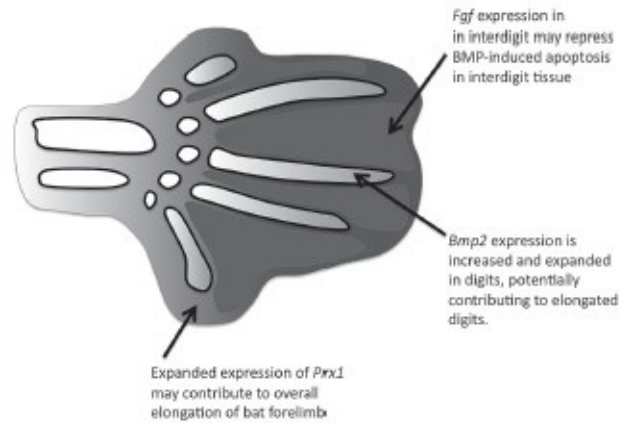


Figure 9-7. Bat Wing. The expression domains of some of the key genes involved in the development of the bat wing.

Without *Gremlin* and *Fgf8*, bats might have long fingers but no wings! Naturally the question arises: How could selection for a longer digit have occurred unless the antagonists to the apoptotic activity of *Bmp2* were already in place? As Norberto Giannini comments:

Some of the regulatory effects that generate an elongated and webbed hand are *intrinsically antagonistic* if not for the rather elaborate patterning of expression in the developing handplate. For instance, an up-regulated *Bmp2* [increased level] is required to elongate the digits, but its expression causes cell death in the interdigital tissue; so specific patterning and additional regulators are required to produce elongated digits *and* dactylopatagium [the membranes between the digits].¹⁰⁰

This implies that the actualization of this remarkable novelty has involved what would appear to be complex simultaneous compensatory recruitment of new gene circuits, which operate in unison to generate long fingers and the intervening webbing—a finding at odds with the Darwinian conception that novelties emerged gradually via a succession of *individual genetic changes*.

As remarked in Chapter 5 in the discussion of “evo-devo,” the mere listing of an inventory of changes that accompanied the actualization of a taxon-defining novelty, like the bat’s wing, provides not the slightest support for Darwinian gradualism. Only by showing that the developmental genetic changes occurred successively, and by identifying and listing the successive changes (one, two, three, four, five, six, etc.), can the Darwinian thesis be confirmed. The fact that we have a description of some of the developmental changes that accompanied the origin of the bat’s wing provides very little insight into how the transition occurred. But one obvious implication of the emerging evo-devo description is that to cross what seems to be on morphological grounds a functional dis-continuum¹⁰¹ (from gliding to powered flight) necessitated coordinated and compensatory changes in many different gene circuits, some of which must have occurred simultaneously—an implication that points away from gradualism to saltation; and this is where the fossil evidence also seems to point. From the complexity of the required changes, and from the fact that some may have had to occur simultaneously, it seems clear why only *one lineage* of mammals managed to convert a standard hand into a wing capable of powered flight.¹⁰² The possibility that the bat hand-wing emerged relatively suddenly is conceded by the authors of a recent paper who speculate that “rapid change from arm to wing morphology

may have resulted from many independently arising predispositions toward longer limbs accumulating in a population over a long period of time. Each of these modifications would individually cause minor or transient effects on limb phenotype due to the buffering effect on phenotypic output by canalization of developmental mechanisms. Once combined in a bat ancestor, however, the cumulative effect could override genetic capacitance *to produce a large and seemingly instantaneous change* at the morphological level.”¹⁰³

Here is how things stand at present: The empirical gap (in the fossil record) between the bat’s wing and the standard mammalian forelimb is every bit as obvious as in 1985. Further, conceiving how the *morphological changes* might have come about gradually, in terms of a long sequence of adaptive intermediates, was always problematical, and the new evo-devo evidence, which shows that the changes involved complex rewiring and integration of novel gene circuits to coordinate the necessary changes in the developing wing, provides no evidence whatsoever for the gradualistic scenario.

Of course, the gradualistic scenario is not “disproved,” and the majority of students of bat evolution—including Norberto Giannini, whom I have cited and quoted extensively above, and most of the other authors in the collection in which his paper appears (*The Evolutionary History of Bats*)—are committed to the gradualist Darwinian scenario. A great deal of further work, to document the full inventory of developmental changes necessary to convert a mouse’s foot into a bat’s wing, will be necessary to determine whether or not the transition could plausibly have come about via a series of tiny adaptive steps.

No matter how incongruous it might seem to the defenders of the Darwinian faith, the evidence as it stands, both fossil and evo-devo, is entirely consistent with a saltational scenario. One cannot dismiss the possibility that the bats acquired their wings relatively suddenly, as seems to be the case with the evolutionary novelties discussed above: the enucleate red cell, the tetrapod limb, the feather, the angiosperm *Bau-plan*, etc.

9.4 The Life Cycle of the European Freshwater Eel

Sigmund Freud is best known as the founding father of psychoanalysis and for his contribution to psychology and psychiatry; yet curiously, his very first scientific paper (published in 1877) dealt with a topic far removed from matters of the mind—the reproductive biology of the European freshwater eel.¹⁰⁴ The reproductive and life cycle of the eel were a complete mystery at the time; no one had seen eels mate or spawn, and the breeding grounds where this takes place were a complete mystery (a mystery only solved in the mid-twentieth century).¹⁰⁵ Further, no one had seen an eel egg or sperm, and as James Prosek comments: “No one could say for sure whether eels even had gender because no one could identify their reproductive organs.”¹⁰⁶ This is not surprising, as we know today that the sex organs of eels mature only after the eels leave fresh waters for the return journey to their oceanic spawning grounds.¹⁰⁷ Even today, “no one has ever been able to find a spawning adult or witness a freshwater eel spawning in the wild. For eel scientists, solving the mystery of eel reproduction remains a kind of holy grail.”¹⁰⁸ It has only been in the past few years that a sexually mature specimen was first obtained in the wild.¹⁰⁹

Considerable kudos, therefore, awaited any young researcher in the late nineteenth century who was able to solve any aspect of the riddle. Working at a marine laboratory in Trieste during the summer of 1876 while still a medical student, Freud dissected many hundreds of eels in an attempt to identify the male gonad and to throw some light on the mysterious reproductive and life cycle of the eel. Freud failed to identify any male organs in any of the eels he dissected that summer, and left Trieste to seek a career in another branch of science. But he did speculate correctly that eels must develop male sexual organs at a later stage in their life cycle.¹¹⁰

The nineteen species¹¹¹ of freshwater eel are found in various parts of the world, including New Zealand, Japan, North America, Europe, and Southern Africa. All share the same basic life cycle (illustrated in Figure 9-8).¹¹² These eels show that taxon-defining novelties or homologs need not be restricted to morphological traits like the enucleate red cell or the pentadactyl limb. Taxon-defining traits (whether of individual species or more inclusive taxa) can also include unique behavioral and reproductive strategies and life cycles. As is well known, there are many species-specific, taxon-defining behavioral traits, as well as weird and wonderful life cycles, particularly among invertebrates such as the blister beetle or liver fluke. The life cycle of the European freshwater eel is merely one example of many baroque taxa-defining homologs that challenge incremental adaptationism.

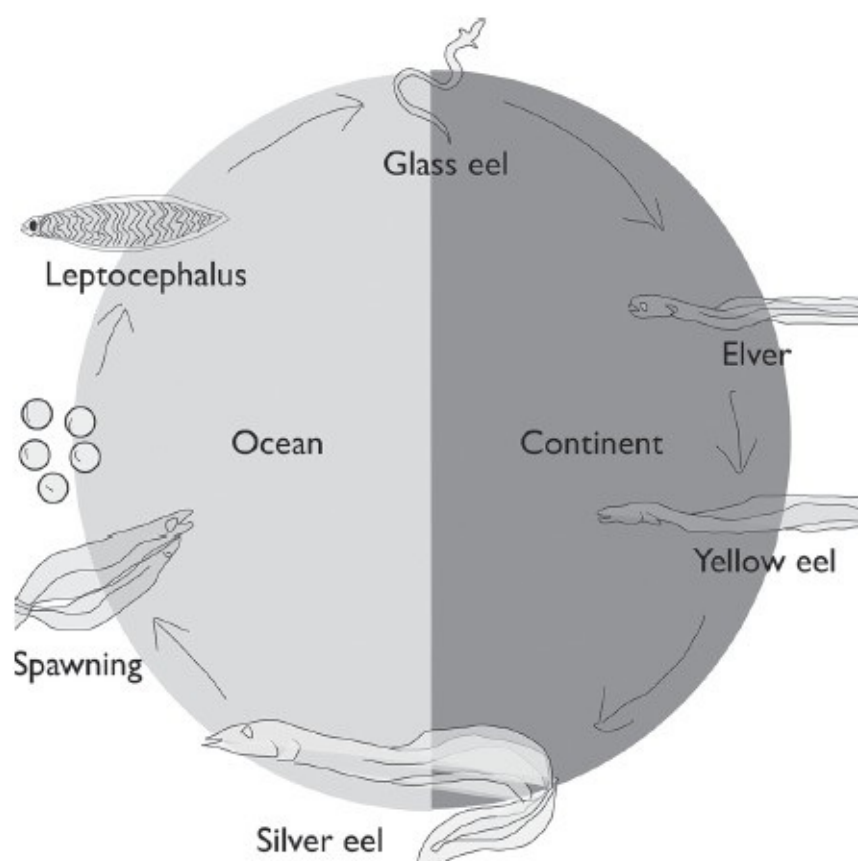


Figure 9-8. Life History of the Freshwater Eel.

We now know something else about eels that Freud could never have imagined: that sex determination in mature freshwater eels is a manifestly baroque phenomenon, one of the most weird and far-fetched of any vertebrate or indeed of any organism, being determined by environmental factors which are still not fully understood.¹¹³ During the maturation of the eel, sexuality is apparently not fixed and environmental factors can

override genetic sex.¹¹⁴ Some studies have found that the proportion of males to females varies in different regions. In the river Elbe, for example, the proportion of males decreases upriver, i.e., with distance from the sea.¹¹⁵ During the maturation of the eel, both sexes, it seems, pass through successive phases of neutrality and juvenile hermaphroditism before finally becoming definitely male or female.¹¹⁶

Their life cycle is no less baroque than their sexual development. The juvenile stages—in which the eels appear as very small, transparent, ribbon-shaped fish known as *Leptocephali* (thin or flat head)—had been familiar to fishermen in the North Atlantic (where they occurred in vast numbers) for centuries; yet until researchers first observed the transformation of *Leptocephali* into recognizable eels in aquariums in the 1890s, these larval forms were considered entirely different species of fish.¹¹⁷ Heroic efforts by the Danish researcher Johannes Schmidt over many years between 1905 and 1930 showed that the very smallest *Leptocephali* were found in the region of the Atlantic known as the Sargasso Sea—a warm body of water off the east coast of the U.S.—which was eventually accepted as the spawning grounds of the eel.¹¹⁸

Although even today, as mentioned above, no one has observed the mating and spawning of freshwater eels in the wild,¹¹⁹ the life cycle is now understood at least in outline. After the eggs hatch in the Sargasso, the tiny *Leptocephali* larvae are carried in the Gulf Stream to the shores of Europe, more than 4,000 kilometers away, over a period of up to a year or more.¹²⁰ As they reach the continental shelf, before commencing their migration up the rivers, they undergo a remarkable metamorphosis. Their body changes from the flat larval form into a cylindrical shape. Their larval teeth are lost, the anus migrates from a sub-terminal position to the abdominal midpoint, and they lose skin pigment and meta-morphose into the well-known cylindrical glass eels,¹²¹ which collect in vast numbers in the estuaries and river mouths of western Europe before commencing their migration upstream. As they enter fresh waters, they gradually lose their glass-like appearance; pigmentation starts to appear in the skin and they take on the more familiar appearance of young eels or elvers.¹²² After a few months of growth, as they move upstream, their pigmentation becomes more marked and they are thereafter known as “yellow eels.”¹²³ During this migration they may travel across wet grass and even dig through wet sand to satisfy their urge to reach upstream headwaters and ponds, thus eventually colonizing every river and small body of water in western Europe.¹²⁴

Prepubertal maturity¹²⁵ is reached in males in about six years and in females in about nine years,¹²⁶ females growing to an average length of about fifty-five centimeters and males to about forty centimeters.¹²⁷ Mature European eels begin their migration back to the Sargasso Sea in autumn and continue into the spring, and again often cross wet grass and surmount all sorts of obstacles including beach walls¹²⁸ in their urge to reach the sea. The females remain three years longer than males before making their way back to the sea.¹²⁹

On leaving for their return journey, they undergo a second metamorphosis; their gut degenerates and they stop feeding¹³⁰ and their pigmentation changes from golden to silvery (hence the term “silver eels”). Silvering involves pigmentation lightening on their sides and ventral surface and darkening on their back to create a countershading pattern to make them difficult to be seen by predators during their long open-ocean migration.¹³¹ Their eyes start to enlarge in size and the eye pigments change for optimal vision in dim blue ocean

light.¹³² The 4,000-kilometer-plus journey back to the Sargasso without feeding and against the current is accompanied by major compensatory metabolic changes to conserve energy for the journey as well as for gonadal maturation.¹³³

Although the life cycle of the European eel is now understood at least in outline, the evolutionary factors that caused such an extraordinarily baroque and roundabout way to bring sperm to egg and complete the reproductive cycle are mystifying. What tiny adaptive steps led from the reproductive habits of a “normal fish” to such a grotesque life cycle consisting of two remarkable metamorphoses? What adaptive significance do the weird sexual metamorphoses serve? What curious series of adaptive steps led to “environmental determination of sex”? Why does the gut shut down and the adults stop feeding to make the journey back to the Sargasso? What contribution to reproductive fitness was made by the migration of the anus from the tail to mid-abdomen as the larvae metamorphosed into glass eels? What conceivable “long series of gradations... each good for its possessor”¹³⁴ (Darwin’s description) could possibly have orchestrated the whole baroque performance? I think it would be hard to invent a story more difficult to account for in terms of cumulative selection.

In contemplating the life cycle of these extraordinary fish, James Prosek was moved to reflect:

We allow ourselves to believe nature can be explained... The eels, through their simplicity of form, their preference for darkness, and their grace of movement in the opposite direction of every other fish, have helped me to see things for which there is no easy classification, things that can’t be quantified or solved, and get to the essence of experience.¹³⁵

The baroque does not end with the Sargasso eel. Anyone who studies the forms of the adult eels and their larvae depicted in any standard text¹³⁶ will be struck by the utterly grotesque phantasms that the forms of eels represent. One species, the so-called “slender snipe eel,” is described briefly by Tim Flannery and Peter Schouten in their book *Astonishing Animals*:

[It lives] nearly two kilometres below the surface of the sea... It has more vertebrae in its backbone—around 750—than any other animal, and can stretch out to a metre and a half long, much of which is its thin tail. Oddly for a creature with such a long body, its anus has evolved by migrating forward and is now situated on its throat. So slender is the fish that even the longest snipe eel weighs less than a hen’s egg.¹³⁷

Just what weird and wonderful combination of selective forces engineered the slender snipe eel? But eels are just the beginning. As Flannery and Schouten describe the denizens of the deep seas:

In the eternal gloom of the deep ocean lives a cast of creatures that seem scarcely believable. Their lives are lived under great constraint, for barely enough food drifts down from the sunlit layers above to keep even the most miserly eater alive. Some are forced to dissolve their skeletons in order to find the nutrients needed to lay eggs, while others may only eat once a year. Most bizarre of all are the net devils or deep sea angler fish... [in some cases] the

male [attaches to the female and degenerates into a wart-like protuberance and is]... reduced to little more than a testicle.¹³⁸

Describing the so-called “gulpers,” Flannery and Schouten write: “After mating gulpers undergo a metamorphosis. In order to find the calcium and energy they required to produce eggs they absorb their own teeth and jaws, thus becoming little more than a sack of jelly.”¹³⁹

Endless similar cases can be cited for which selective explanations seem, as Darwin himself confessed, “awful stretcher[s].”¹⁴⁰ Karl Ludwig von Bertalanffy, a long-time critic of Darwinism, made the point for many skeptics when he confessed:

I, for one, in spite of all the benefits drawn from genetics and the mathematical theory of selection, am still at a loss to understand why it is of selective advantage for the eels of Camacchio to travel perilously to the Sargasso Sea, or why *Ascaris* has to migrate all round the host’s body instead of comfortably settling in the intestine where it belongs; or what was the survival value of a multiple stomach for a cow when a horse, also vegetarian and of comparable size, does very well with a simple stomach; or why certain insects had to develop those admirable mimicries and protective colorations when the common cabbage white butterfly is far more abundant with its conspicuous white wings. One cannot reject these and innumerable similar questions as incompetent; if the selectionist explanation works well in some cases, a selectionist explanation cannot be refused in others.¹⁴¹

10. Bridging Gaps: The Origin of Language

You are mesmerized, not simply by the subtlety of these marvelous engravings... For this is not in any sense crude art; it is art as refined in its own way—and certainly as powerful—as anything achieved since. Any preconceptions you may have had of the “primitiveness” of “cavemen” are instantly dispelled... This remarkable art... we can instinctively recognize... as something profoundly human. Not only is it humans, uniquely, who create art, but it is only we who indulge in behaviors as mysterious and unfathomable as this.

Ian Tattersall, *Becoming Human: Evolution and Human Uniqueness* (1999), Prologue.

On our own kind, *Homo Sapiens*, slipped suddenly into being on the rich, game-laden African grasslands of the late Pleistocene, and spread rapidly over the next 200,000 years to every corner of the world. Here was the greatest of novelties, a new type of being—for the first time a creator and molder of the world—a *speaking and thinking being, knowing, insightful, artistic, and religious*. As well as a hunter, here was a storyteller, a mystic, a seer, and a dreamer.¹ Nothing before in evolution had hinted at the possibility of such a novel organism. The radical nature of this mysterious happening, and the unprecedented intellectual advance it entailed, is shown graphically in the marvelous frescoes of cave art of the upper Paleolithic in Europe.²

10.1 Wallace’s Enigma

One of the most curious features of human evolution, and one which poses at the outset an intriguing and still unanswered challenge to the Darwinian and functionalist narrative, was alluded to by Alfred Russel Wallace more than a century ago. All extant humans, Wallace noted, share the same higher intellectual capabilities, and so, incredible though it may seem—and I think the word *incredible* is well chosen—a brain capable of the intellectual feats of an Einstein, a Newton, or a Mozart must have already emerged in our last common ancestors more than 200,000 years ago.³ But how, Wallace argued, could our love and capacity for abstract thought, for language, for mathematics, for music, and for art have been of utility in that unforgiving environment, *millennia before their utility was manifest*? Such intellectual abilities seem absurdly powerful, beyond any conceivable utility for hunter-gatherers on that ancient savanna, and hence beyond any functionalist explanation.

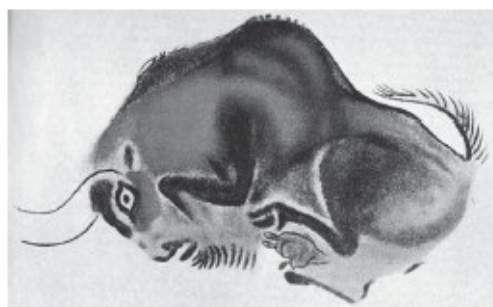


Figure 10-1. The Altamira bull.

In his essay, “The Limits of Natural Selection as Applied to Man,” Wallace stressed

that natural selection cannot bring about any adaptation unless “it is for the good of the being so modified.”⁴ So how, he asks, did a “surplusage” of intellectual powers, far beyond the need of ancient man, come about by natural selection? How could it have brought into being the mathematical abilities of an Einstein or the musical abilities of a Mozart, extraordinary talents which remained latent for vast periods of time, only to become manifest in modern times? In his words:

It is evident... that the absolute bulk of the brain is not necessarily much less in savage than in civilised man... But what is still more extraordinary, the few remains yet known of pre-historic man do not indicate any material diminution in the size of the brain case.⁵

We are... driven to the conclusion that in his large and well-developed brain he possesses an organ quite disproportionate to his actual requirements—an organ that seems prepared in advance, only to be fully utilized as he progresses in civilization.⁶

As Noam Chomsky recently commented: “[Wallace] recognized that mathematical capacities [for example] could not have developed by natural selection; it’s impossible, because everybody’s got them, and nobody’s ever used them, except for some very tiny fringe of people in very recent times. Plainly, they developed in some other way.”⁷

It is certainly mysterious that, although the human intellect was already on the ancient savanna fully-developed and prepared for its subsequent intellectual journey, equipped with all the basic linguistic and cognitive insights that all modern humans share, *it lay dormant for millennia*. The great frescoes of Lascaux, Combarelles, and Altamira (see Figure [10-1](#)) were painted only 30,000 years ago, eons after their ancestors had departed their African homeland. It was only 5,000 years ago when linguistic symbols were first written down in scribbles and hieroglyphics. And it was only during the past 500 years that humans finally began to use their intellects to uncover the laws of nature, to unlock the secrets of the heavens, to measure the diameter of galaxies, and to probe into the heart of the atom. Yet the biological capacity for such achievements was there all along.

From an evolutionary point of view, the origin of man’s higher intellectual abilities is one of the greatest of all mysteries, of all facts to be explained. It would certainly seem, in light of these preliminary observations, that *the origin and evolution of our intellectual powers must have involved causal factors beyond natural selection*.

10.2 The Earliest Modern Human Beings

Pinpointing the date of the last common ancestor of modern humans, and the date by which the mental abilities and linguistic abilities of modern humans had already emerged, is complicated by uncertainty about the linguistic abilities and intelligence of archaic humans such as Neanderthals and Denisovans, who interbred with modern humans *after* our ancestors left Africa. On the grounds of the normal definition of a species as an interbreeding population of organisms, Neanderthals and Denisovans must be classed as subspecies or races of *Homo sapiens*, and this would suggest that they may also have had language and relatively high intelligence. Although it is controversial, the most recent evidence points in this direction.⁸ And if indeed Neanderthals had language and an

intelligence level comparable with that of modern humans, it must be inferred that at least some of our mental and perhaps also our linguistic abilities predate the last common ancestor of modern and archaic humans about 500,000 years ago.⁹

The fact that the amino acid sequences of the *FOXP2* gene in Neanderthals, Denisovans, and modern humans all differ at the same two amino acid positions from the same gene in the chimpanzee is suggestive.¹⁰ Mutations in *FOXP2* cause language disorders in modern humans, although precisely what role this gene plays in language development is controversial. Recent evidence suggests that it is a gene which affects linguistic competence indirectly via pleiotropic influences on many different aspects of brain development. (See discussion below.)

Further support for the claim that Neanderthals were fully human is the fact that their technology was more complex than that of some isolated modern human groups. They built houses, made clothes, used fire, made bone and stone tools, buried their dead, and constructed boats.¹¹

In these arts they were probably in advance of modern Andaman islanders and Tasmanian aborigines.¹²

We are thus faced with the possibility that humans with fully modern linguistic capacity emerged as far back as 500,000 years ago.

10.3 Lack of Homolog

Some of our mental abilities and emotional traits are certainly shared to some degree by other species,¹³ but language, as Chomsky comments, is *without any homolog in any other species*.¹⁴ Language is a Type-defining homolog, restricted to an individual species, an autapomorphy in cladistic terminology, and like other such homologs, it is not led up to by any empirically known sequence (e.g., starting with simple “grunts and gestures” and progressing through more and more complex communication systems till we reach human language). And again—a recurring theme of this book—*no plausible hypothetical evolutionary series has ever been proposed*.¹⁵ Thus, just as in the case of the other defining novelties discussed above, the evidence is consistent with a saltational origin.

Because of the lack of homology and the lack of plausible adaptive evolutionary steps, the origin of language remains an abiding mystery. The authors of a recent paper comment:

Understanding the evolution of language requires evidence regarding origins and processes that led to change. In the last 40 years, there has been an explosion of research on this problem as well as a sense that considerable progress has been made. We argue instead that the richness of ideas is accompanied by a poverty of evidence, with essentially no explanation of how and why our linguistic computations and representations evolved.¹⁶

10.4 Universal Grammar

In the early 1960s, in one of the landmark advances in twentieth-century science, Noam Chomsky showed that all human languages share a deep invariant structure. Despite their very different “surface” grammars, they all share a deep set of syntactic rules and

organizing principles. All have rules limiting sentence length and structure and all exhibit the phenomenon of recursion—the embedding of one sentence in another.¹⁷ Chomsky has postulated that this deep “universal grammar” is innate and is embedded somewhere in the neuronal circuitry of the human brain in a language organ. Children learn [human] languages so easily, despite “the poverty of stimulus,”¹⁸ because they possess innate knowledge of the deep rules and principles of human language and can select, from all the sentences that come to their minds, only those that conform to a “deep structure” encoded in the brain’s circuits.¹⁹

There is considerable controversy over what structures in the brain restrict all human languages to the same deep structure. Some linguists reject an innate neurological organ devoted specifically to language. Conceiving that it is only the brain’s *general* abilities that are “pre-organized,” they envisage language as a learned skill based on a “functional language system” and design constraints, distributed across numerous cortical and subcortical structures.²⁰

Yet, however it is derived during development, there is no doubt that a unique deep structure underlies the languages of all members of our species, modern *Homo sapiens*.²¹ It is because of the same underlying deep structure that we can speak the language of the San Bushman or an Australian aborigine, and they in turn can speak English. The fact that all modern humans, despite their long “evolutionary separation”—some modern races such as the San of the Kalahari and the Australian aborigines have been separated by perhaps 400,000 years of independent evolution—can learn each other’s languages implies that this deep grammar *must* have remained unchanged since all modern humans (African and non-African) diverged from their last common African ancestor, at least 200,000 years ago. As Chomsky puts it:

What we call “primitive people”... to all intents and purposes are identical to us. There’s no cognitively significant genetic difference anyone can tell. If they happened to be here, they would become one of us, and they would speak English; if we were there, we would speak their languages. So far as anyone knows, there is virtually no detectable genetic difference across the species that is language-related.²²



Figure 10-2. San Bushman of the Kalahari Making a Fire.

As mentioned above, it is not only the deep structure of language that has remained invariant across all human races. All races share in equal measure *all the other higher intellectual abilities: musical, artistic, and mathematical ability, and capacity for abstract thought*. These also, therefore, must have been, as mentioned above, present in our African common ancestors more than 200,000 or more years ago, and must also have remained unchanged, and for some reason latent, since our common divergence. To

suggest that language and our higher mental faculties evolved in parallel to reach these same remarkable ends independently in all the diverse lineages of modern humans over 200,000 years ago or more would be to propose the most striking instance of parallel evolution in the entire history of life, a thing inexplicable in Darwinian terms.

10.5 Complexity

One aspect of language that no one will dispute is that linguistic competence depends on a set of extraordinarily complex neural circuits in the brain. Some idea of the very great complexity that underlies language processing is conveyed with great clarity in Stephen Pinker's *The Language Instinct*. In his words:

[Language processing involves] many parts: syntax, with its discrete combinatorial system building phrase structures; morphology, a second combinatorial system building words; a capacious lexicon; a revamped vocal tract; phonological rules and structures; speech perception; parsing algorithms; learning algorithms. Those parts are physically realized as intricately structured neural circuits... What these circuits make possible is an extraordinary gift: the ability to dispatch an infinite number of precisely structured thoughts from head to head by modulating exhaled breath.²³

Linguistic processing involves the integration of many separate subordinate operations carried out in distinct modules in the brain, each devoted to a very specific aspect of linguistic processing. As Pinker points out, "There must be portions of the cortex which carry out circumscribed tasks, because brain damage can lead to language deficits [aphasias] which are startlingly specific."²⁴ Pinker gives some examples, such as the "pure word" syndrome:

The patients can read and speak, and can recognize environmental sounds like music, slamming doors, and animal cries, but cannot recognize spoken words; words are as meaningless as if they were from a foreign language. Among patients with problems in grammar, some do not display the halting articulation of Broca's aphasia but produce fluent ungrammatical speech. Some aphasics leave out verbs, inflections, and function words; others use the wrong ones. Some cannot comprehend complicated sentences involving traces (like *The man who the woman kissed* (trace) *hugged the child*) but can comprehend complex sentences involving reflexives (like *The girl said that the woman washed herself*). Other patients do the reverse.²⁵

Confirmation that language processing is modular, involving tiny regions of the brain devoted to specific subtasks, comes also from experiments where different regions of the brain are directly stimulated (electrically) in conscious patients. Amazingly, as Pinker points out, "Stimulating [regions]... no more than a few millimeters across could disrupt a single function, like repeating or completing a sentence, naming an object, or reading a word."²⁶ Just how extraordinarily complex is the parsing and processing by the special sets of neuron banks in the cortex is succinctly conveyed by Pinker in Chapter 10 of *The Language Instinct* (see his diagram on page 326 of that book).

An intriguing indication of the obtuse complexity of the language organ is the fact that even after tremendous efforts, stretching back over sixty years, no computer can be

taught to understand and correctly interpret human language. We are a long way past 2001, and still in 2015 there is no HAL (the supercomputer in the film *2001*) or any computer with a deep understanding of human language. The author of a recent web posting regarding the Loebner Prize (offered to anyone who can program a computer to understand human language) writes:

The Loebner Prize is a competition of the world's best "chatbots"—computer programs designed to simulate how a human interacts in a normal written conversation—that promises a grand prize of US \$100,000 to the first program that can interact with another human in a natural way, undistinguishable from another human. The competition started in 1991, but the prize is still up for grabs and the transcripts from each year's winners tell us just how far we are (the answer: very) from ever reaching that goal.²⁷

Given the vast number of exquisitely specific types of aphasias,²⁸ and the necessity for horrendously complex neural circuits (or neural modules) to carry out the syntactical analysis (parsing) of symbol strings (the sequence of words in sentences), and the intractable difficulty of simulating language in a machine, we can safely conclude that the language organ *is very complex*. Indeed, it may be the most complex adaptation in all of nature, an adaptation that, in the words of Peter MacNeilage, "dwarfs most other evolutionary achievements."²⁹

The failure to simulate linguistic competence in a computer not only underlines just how complex the underlying processing machinery must be, but at the same time raises a curious Darwinian paradox. *How could blind unintelligent cumulative selection, the blind watchmaker, have assembled a device—the language organ—of such complexity and sophistication that intelligent humans cannot "intelligently" simulate these unique abilities in a machine?*

10.6 Did Language Arise Per Saltum?

As is well known, Chomsky sees the origin of language in strikingly internalist and saltational terms, as the result of the sudden self-organization of the brain's neuronal circuits. He writes: "There was a sudden 'great leap' forward... some small mutation took place... in a *single person*. Something happened in a person that that person transmitted to its offspring. And... in a very short time, it dominated the group."³⁰

Note that for Chomsky, the emergent leap forward might have been triggered by selection for bigger brains,³¹ and thus:

It is perfectly safe to attribute this development [of innate mental structure] to "natural selection," so long as we realize that there is no substance to this assertion, that it amounts to nothing more than a belief that there is some naturalistic explanation for these phenomena... In studying the evolution of mind, we cannot guess to what extent there are physically possible alternatives to, say, transformational generative grammar, for an organism meeting certain other physical conditions characteristic of humans. Conceivably, there are none—or very few—in which case, talk about the evolution of language capacity is beside the point.³²

Ian Tattersall was also inclined to an emergentist, saltational view of human origins, especially of our artistic and intellectual abilities. In *Becoming Human* he comments on human uniqueness:

The “human capacity” is not simply an extrapolation of the earlier trends in our lineage... It is more akin to an “emergent quality,” whereby... a new combination of features produces totally unexpected results. The classic example of such a quality is water, whose remarkable characteristics, so essential for life, are entirely unpredicted by those of either hydrogen or oxygen atoms alone.³³

Therefore, rather than being earned over thousands of generations, involving tens of thousands of genetic substitutions, novel genes, and the selective culling of millions of the unfit, linguistic capacity was *given*. The subhuman primate brain was already “predisposed” for the self-organizing phase transition to abstract thought and symbolic reference, necessitating only, as Tattersall comments, “a change that was presumably *rather minor in genetic terms*. Just as the keystone of an arch is a tiny portion of the whole structure yet is vital to its integrity, a relatively small neural change must have had this remarkable emergent effect in our brains.”³⁴ Tattersall confesses that just why the primate brain was so pre-figured is a mystery.³⁵

Even Gould was inclined to the emergentist, internalist view. In *The Richness of Life* he speculates:

Complex objects often display the interesting and paradoxical property of major effect for apparently trifling input... Perhaps... the origin of human consciousness, required little more than an increase of brain power to a level where internal connections became rich and varied enough to force this seminal transition.³⁶

How quickly language and our higher intellectual abilities were acquired is of course unknown, and Chomsky’s saltational/emergentist view is very controversial. Most researchers in this area believe, in conformity with the Darwinian framework, that language came about gradually, by cumulative natural selection.³⁷ Against this, Chomsky remarks:

The overwhelming assumption is that language evolved slowly through natural selection. Yet that doesn’t seem at all consistent with even the most basic facts. If you look at the literature on the evolution of language, it’s all about how language could have evolved from gestures, or from throwing, or something like chewing, or whatever. None of which makes any sense.³⁸

As in the cases of the other novelties discussed above, a plausible gradualist scenario for the origin of language has never been presented. I am not aware of any author, including Terrence Deacon and Stephen Pinker, who has shown even in vague outline how the various rules of the universal grammar (rules restricting sentence length, rules for negation, for recursion, etc.) might have come about by mutation, gene by gene, over thousands of generations and become gradually embedded in specific neural circuits in the brain.

Take one characteristic that all human languages exhibit: recursion, i.e., sentences

embedded within other sentences. In the sentence, “The man *who was wearing a blue hat which he bought from the girl who sat on the wall* was six feet tall,” the italicized words are embedded sentences. Special rules allow human speakers to handle and understand such sentences. And these rules, which govern the nature of recursion, are specific and complex. So how did the computational machinery to handle it evolve? David Premack is skeptical:

I challenge the reader to reconstruct the scenario that would confer selective fitness on recursiveness. Language evolved, it is conjectured, at a time when humans or protohumans were hunting mastodons... Would it be a great advantage for one of our ancestors squatting alongside the embers, to be able to remark, “Beware of the short beast whose front hoof Bob cracked when, having forgotten his own spear back at camp, he got in a glancing blow with the dull spear he borrowed from Jack”?

Human language is an embarrassment for evolutionary theory because it is vastly more powerful than one can account for in terms of selective fitness. A semantic language with simple mapping rules, of a kind one might suppose that the chimpanzee would have, appears to confer all the advantages one normally associates with discussions of mastodon hunting or the like. For discussions of that kind, syntactical classes, structure-dependent rules, recursion and the rest, are overly powerful devices, absurdly so.³⁹

One reason to be very skeptical of the Darwinian claim that the deep structure of human language came about as a result of bit-by-bit, incremental selection of tiny advantageous mutations over millions of generations is its mysterious *invariance in all human lineages since it emerged 200,000 years ago* (and as far as we can tell *the invariance of all the higher intellectual traits and characteristics which make every living human instantly recognizable as belonging to our species*). In this, language (and what we may term “human nature”) resembles the other taxa-defining novelties, all of which exhibit the same mysterious, robust invariance since their first appearance. If the language organ was put together gradually under selective guidance and direction between 2,300,000 and 200,000 years ago (500,000 years ago if Neanderthals shared our linguistic ability) and represents what is essentially a mere “contingent complex,” why did the process come to such a sudden halt? On any Darwinian view, the grammar of language and our higher intellectual traits might be expected to continue to undergo adaptive change in all the divergent lineages since the great diaspora as different races acquired different intellectual attributes. In this, language represents another classic *Bauplan* like the pentadactyl limb, where a taxon-defining novelty (or suite of novelties, including language and other associated higher mental faculties) has remained invariant since its origin, frozen as it were in all the divergent lineages which inherited it from their last common ancestor. This observation is entirely consistent with the structuralist notion that the language organ, like the other taxa-defining novelties, possesses a special natural robustness and is no trivial contingent assemblage.

10.7 The Elusive Language Genes

Despite the fantastic complexity of the language organ, perhaps the most complex entity in all nature, described so lucidly by Pinker,⁴⁰ Darwinism implies it came about as a result of

hard-earned cumulative selection, bit by adaptive bit, neural circuit by neural circuit, gene by gene, generation after generation, to serve functional ends. But if indeed the language organ is a “Darwinian contingent assemblage” and not, as structuralism infers, the emergent natural product of internal causal factors unique to the primate brain, then it must be specified in its entirety in exhausting detail in a blueprint in the genes. And it follows that, if there are no “language genes,” i.e., genes specifying in detail the different processing modules of the language organ or apparatus, then Chomsky “wins by default” and the origin of language must be presumed to be an emergent epigenetic phenomenon, the result of non-Darwinian higher-order self-organizing internal processes in the brain. Small wonder, then, that the search for language genes became the holy grail of biologists seeking a reductionist Darwinian account of human origins.

a. Population Genetics

One suggestive preliminary observation which undermines the notion of a vast inventory of genetic elements specifying in detail the language organ and which supports the alternative emergentist position is that despite the exceptional nature of our linguistic (and intellectual) abilities, and despite our possession, in the language organ, of one of the most complex adaptations in all nature, *the genetic difference between man and chimpanzee is no more than that between many other well-defined species in nature*, and lies in the range of four to five percent,⁴¹ less than that reported between mouse and rat and dog and fox.⁴² These comparisons provide no hint that the human genome is burdened by the need for a vast inventory of novel genes to specify a uniquely complex adaptation.

Another significant pointer away from an imaginary vast inventory of language genes is the fact that the time-span available for assembling the human mental and linguistic apparatus is measured in only a few million years, a mere instant of geological time. This weakens the plausibility of the Darwinian model, since on Darwinian principles, the accumulation of a countless series of adaptive mutations to specify *the most complex organ in the universe* should have taken *an immense period of time*.

Moreover, the short length of time is not the only problem. Our ancestral lineage during those few million years involved tiny population numbers, and long generation times, undermining further the plausibility of the conventional Darwinian view. Why? Because it is universally acknowledged that beneficial or adaptive mutations are rare, and consequently, as population geneticist John Hawks points out in a recent *Scientific American* issue on human evolution,⁴³ they are much more likely to occur in large populations (which our ancestors did not have) than small ones. And if the generation time is also long, then the likelihood of new mutations *per unit of time* is diminished further.

In passing, it is interesting to note that Darwin also saw long periods of time and large population numbers as enhancing the likelihood of evolutionary innovation, as both factors increased the likelihood of favorable variations.⁴⁴

In the same *Scientific American* article, John Hawks describes a number of specific adaptive mutations which have occurred in human populations over the past 30,000 years: for lactose tolerance (for milk-drinkers, to prolong their use of milk into adulthood), for multiple amylase genes (to assist in the digestion of starch after the advent of farming), for fair skin (to promote Vitamin D synthesis by sunlight in inhabitants of higher, less sunny

latitudes), and for sickle-cell hemoglobin (to protect against malaria). These have only occurred because of the thousand-fold increase in human population over the past 30,000 years.⁴⁵ During this time increasing population size gave our ancestors “many more rolls of the dice,”⁴⁶ increasing the likelihood of finding and establishing new adaptive mutations. As Hawks comments: “As human populations [over the past 30,000 years] have spread into new parts of the world and grown larger, they have rapidly adapted to their new homes precisely because those populations were so big.”⁴⁷

Many studies suggest that the effective population of humans throughout the Pleistocene, i.e., before the recent expansion that Hawks refers to, was on the order of 10,000.⁴⁸ This means that over most of the past three million years of human evolution, especially during the two million years when brain size was dramatically increasing and when our cognitive and linguistic abilities were emerging,⁴⁹ population numbers were vastly smaller than today, and vastly smaller than those late Pleistocene populations which acquired lactose tolerance and sickle-cell hemoglobin. Thus, over most of the course of human evolution, the potential “rolls of the dice” were only a fraction of those possible in modern populations.

In addition to the rarity of advantageous mutations, in small populations, chance rather than selection tends to determine whether or not an adaptive mutation is substituted in the population. As Laurent Duret points out in a *Nature Education* article: “In small populations, the stochastic effects of random genetic drift overcome the effects of selection.”⁵⁰ Life was precarious in Pleistocene times when linguistic ability was emerging, and the human population was split into small, isolated tribes, which would have hovered continually on the edge of extinction, especially in times of drought or other environmental challenges. Thus, even if an unlikely adaptive mutation occurred, the mutation probably would be lost to the human lineage, either because the individual bearing the mutation failed to pass it on to his or her offspring or because the tribe itself became extinct. There is nothing controversial about this. Because of the very small interbreeding populations along the lineage leading to modern man, the human genome must have been shaped mainly by genetic drift rather than selection.

Irrespective of the question as to the relative significance of drift or selection in shaping the human genome, as far as finding adaptive mutations is concerned there is no doubt that the larger the population size, the greater the chance of success. Thus, bacteria are much better Darwinian evolutionary engines than primates. In the search of genetic space for novel adaptive mutations, almost any bacterial population will outperform any primate population by many orders of magnitude. For example, the total number of bacteria in the human gut is commonly reported to be about 100 trillion, and the total gene complement of the gut metagenome is 150 times that of the human genome.⁵¹ Even on the conservative assumption that each bacterium undergoes one mutation each day, in each human gut more changes are rung in DNA sequences per day—more “rolls of the dice”—than could possibly have occurred during primate evolution in the two million years preceding the origin of man. Because of the small population numbers, long generation times, and short time period involved, humans provide *almost the worst imaginable scenario for the evolution by natural selection of complex adaptations and especially our cognitive and linguistic abilities*. If you had to choose to play the blind watchmaker and re-engineer by trial and error a complex new adaptive trait—especially one *whose*

complexity dwarfs that of any other adaptation in nature—you would choose to work with an organism like *E. coli*, or a mouse, or even a monkey, but not a human or any of sort of higher primate.

Overall, the constraints of population genetics point strongly away from the Darwinian conception of language competence as a product of hard-earned adaptive evolution and away from the existence of a bank of genes specifically devoted to assembling the language organ in the brain. They provide powerful support for Alfred Wallace's and Noam Chomsky's inference that *internal factors, in addition to selection for functional ends, were responsible for the origin of our linguistic and cognitive abilities.*

b. Comparative Genomics

Despite the negative implications of population genetics, after the publication of the draft genome of the chimpanzee was published in 2005, the prospect was raised that at last the elusive language genes might be identified. But it was not to be! Comparisons between the two genomes showed that of the 20,000 or so protein-coding genes in man and chimpanzee, only a relatively small fraction show any significant sequential differences, and only a handful of genes identified in the human genome are not present in chimpanzee and *vice-versa*. Further, of those human genes that seem to have been under selective surveillance since our lineage diverged from that of the chimpanzee, many have no apparent relationship to language or neural development.⁵² The genes that display the clearest evidence of positive selection, i.e., that have a high *KA/KS* ratio,⁵³ are mostly related to host-pathogen interaction, immunity, reproduction, and energy production.⁵⁴

The human brain uses a considerable amount of metabolic energy, and selection for more efficient energy utilization makes sense given the increase in the size of the human brain and increase in neuron number over the past few million years.⁵⁵ Because our brain is three times the size of a chimpanzee's, it would be expected that there would be some genes involved in neural ontogeny that exhibit sequential differences and differences in gene expression compared to those in the chimpanzee.⁵⁶ But there is no evidence that any of such genetic differences are involved in specifying the language organ. As Todd Preuss comments in a recent *PNAS* paper, the fact that human brains are “running hot” does not imply that selection for energy generation had any direct causal connection with the origin of our unique intellectual abilities.⁵⁷

Overall, the comparisons of the human and chimpanzee genomes have proved a great disappointment for those seeking to find the source of our uniqueness and linguistic competence in the genes.⁵⁸

c. FOXP2

The most celebrated example of a putative language gene that has undergone change in our lineage (and in Neanderthals) is *FOXP2*. Mutations in this gene cause speech impairment in human families and were first identified through a well-known genetic study of a British family of Pakistani origin, the so-called “KE family.” The gene in humans differs at two amino acid positions from that in the chimpanzee. Although it has been widely touted as a *language gene* and as providing evidence that there is a genetic basis for human language acquisition, the case is far from established. As Todd Preuss comments:

Important questions remain. For one, were the sequence changes in human *FOXP2* driven by selection for speech or language ability? This is not necessarily the case... There is still no clear or direct connection between the human-specific amino acid substitutions in *FOXP2* and speech or language—not from the comparative studies, nor from the mouse-model studies, nor from the gene expression studies. The fact that mutations of *FOXP2* in humans result in speech impairments shows that it plays a role in speech development, but the nature of its role remains unclear.⁵⁹

There is a further complication in the connection between *FOXP2* and language:

Examination of fetal human brain tissue also makes it clear that *FOXP2* expression is not limited to brain regions usually associated with language. For example, although it is expressed in the perisylvian cortical region (the cortex spanning the territory from Broca's to Wernicke's language areas), and is present in the striatum (caudate and putamen), as one might expect from neuroimaging studies of the KE family, it is expressed in the cortex of frontal pole and occipital pole, neither of which are critical for language. *FOXP2* is also expressed in the thalamus, cerebellum, and brain stem, and moreover, is expressed in a wide variety of tissues other than the brain.⁶⁰

As Preuss cautions, it is not clear that changes in the amino acid sequence of *FOXP2* were specifically selected for their effect on the development of language.⁶¹ Indeed, the evidence suggested even before the identification of the *FOXP2* gene that the inherited disorder in the KE family had “a broad phenotype which transcends impaired generation of syntactical rules and includes striking articulatory impairment as well as deficits in intellectual, linguistic and orofacial praxic [motor skill] functions generally.”⁶² And subsequent work on the family has shown that “the verbal and non-verbal deficits arise from a common impairment in the ability to sequence movement or in procedural learning”⁶³ and that “the claim that this family [KE] has a specific deficit in morphosyntactic rule use is therefore untenable.”⁶⁴

Other genes that appear to cause specific language impairment are *CNTNAP2*, *ATP2C2*, and *CMIP*.⁶⁵ But again, whether these genes are uniquely involved in specifying components of the language organ or are generalists—genes involved in fundamental aspects of neurogenesis—remains an open question.⁶⁶ Van der Lely and Pinker concur; as they point out, like *FOXP2* these genes have other functions: “[They] appear to affect early embryonic development... During cortical neurogenesis they are expressed in similar brain regions, including deep layers of the cerebral cortex, striatum and cerebellum, presumably leading to abnormal neurobiological pathways later in life.”⁶⁷

The absolute failure to date to find a *single* gene or any genomic factor, let alone the imagined vast inventory of genes that on any gene-centric mechanistic view would be necessary to specify the most complex adaptation in nature, must stand as one of the greatest recent disappointments of reductive materialism and gene-centrism. This failure must be taken as strong evidence against the complex genetic reconfiguring of a million and one neural circuits to assemble bit by bit the language organ under the direction of cumulative selection. In one recent *PNAS* paper discussing the “differences” in the genes between man and chimpanzee, the authors concede, in words that eerily echo Chomsky

and concur with structuralism and emergentist notions, that in the face of genomic comparisons, “we would not be surprised if phylogenomic studies reveal that... the modern human mind differs from the other species primarily because of the modern human brain’s *larger number of neurons and dendritic connections* and much longer periods of postnatal development in a social nurturing environment.”⁶⁸

Altogether, the current genetic evidence adds up to what is in effect a structuralist’s manifesto, because it suggests that our linguistic ability and intellect is not the result of a hard-earned, gradual, complex neuronal rewiring under the direction of natural selection under those ancient African skies. Rather, all the evidence points to the Chomsky model, in which human language is an epigenetic, emergent phenomenon arising from a currently elusive self-organizational mechanism in the primate brain. Chomsky proposes that “some small genetic change led to the rewiring of the brain that made this human capacity available.”⁶⁹

The small genetic difference between chimpanzee and man is perfectly explicable if the differences between the chimpanzee and human brain, responsible for the emergence of language and our higher intellectual faculties, *are emergent, arising primarily from self-organizational processes and not from genetic tinkering*. There is nothing anomalous about this. Many self-organized systems exhibit what is termed self-organized criticality, the metastable point or tipping point when the tiniest change can cause a dramatic cascade of changes which reorganize the whole system—like the spark which initiates a forest fire, like the single grain of sand which initiates an avalanche in a pile of sand, and like the imperceptible movement in a tectonic plate which initiates a devastating earthquake.

10.8 Brain Development

Given the overwhelming evidence that much higher-order organic form is emergent and epigenetic, arising from self-organizational processes during development and *not* specified in the genes,⁷⁰ it is curious (to say the least) that students of human evolution should have ever thought of scrutinizing genes for the signatures of human uniqueness. The gene-centric perception was already in effect well past its “use by” date even in 2005 when the sequence of the chimp genome was first published, and it should have been quite self-evident that scrutinizing genes, including regulatory genes and the so called “dark matter” of the genome, no matter how exhaustive the analysis, is *never* going to provide a complete account of our origin or ontological status. Even the 3-D spatial arrangement of atoms in an individual protein is not specified directly in the amino acid sequence (see Chapter 13, section 13.2e).

That the assembly of brain and nerve circuits which underlie our high cognitive and linguistic ability is bound to involve, as is universally true of so much of the higher architecture of life, *emergent, self-organizing processes invisible from the genes* is now widely acknowledged, as, e.g., by MacNeilage:

We find consensus in the diverse fields of evolutionary biology... molecular biology... neurobiology... neurophysiology, and neurology of language development itself... that the human genes contain insufficient information to specify the structure of the human nervous system which comprises several billion cells, each having, on average, several hundred connection with other

cells. In addition to the informational poverty of the genes, Stent (1981) also emphasizes what could be called the enormous causal distance between genes and the eventual structure of the nervous system in particular: “[T]he role of genes... is too many removes from the processes that actually ‘build nerve cells and specify neural circuits that underlie behavior’ to provide an appropriate conceptual structure for posing the developmental questions that need to be answered.”²¹

Although no one knows how the “language organ” might have arisen in phylogeny, we do know something about how it arises in ontogeny, and what we know points to self-organization, not specification in a detailed genetic blueprint. The details are at present obscure, but from certain observations it seems that the “language organ” is almost entirely the result of the self-organizing abilities of the brain itself. The fact that no genetic mutations have ever been observed to cause the sorts of specific defects in brain processing which follow from brain lesions in the adult brain is very suggestive.²² This provides powerful indirect evidence that the modules in the adult brain are not specified in the genes but arise entirely from higher organizational phenomena during development, i.e., *they are strongly emergent*. Exactly this point was emphasized in a paper by Annette Karmiloff-Smith:

We challenge this direct generalisation from adult phenotypic outcomes to genetic specification... While acknowledging that selective deficits in normal adult patients might justify claims about cognitive modularity, we question whether similar, seemingly selective deficits found in genetic disorders can be used to argue that such cognitive modules are pre-specified in infant brains. Cognitive modules are, in our view, the outcome of development, not its starting point.²³

If the order of the language organ is emergent ontologically in humans today, and not specified bit by bit by a blueprint in the genome, this raises the possibility that emergent factors beyond selection were involved in its evolutionary origin—a conclusion consistent with Wallace’s inference discussed in the first section of this chapter and with Chomsky’s saltational view.

There is another line of evidence that supports the self-organizational, emergent paradigm. If the basis of language lay in genetically determined complex neural networks in the left side of the brain, then one might expect that damage to the areas in the left hemisphere known to be involved in language processing, i.e., Wernicke’s and Broca’s areas, would lead to linguistic impairment. While this is true in adults, and explains various aphasias, curiously, children can recover language ability even after these regions are lost. Amazingly, children who have lost their entire left hemisphere (which contains the key regions for language processing in normal adults) are still able to acquire and learn language. Deacon confesses: “The fact that hemispherectomized children can learn any aspect of language is a miracle....”²⁴ And later in the same work he concludes: “We are not adapted just for symbolic learning but *for fail-safe symbolic learning*.”²⁵ This is a phenomenal case of robust self-organization—the regeneration of the entire language organ via a novel route—and constitutes dramatic evidence that the generation of the language organ is primarily a matter of neural self-organization rather than of detailed

genetic specification. The ability of children to reconstitute the language organ in a different part of the brain is an example of the profound general plasticity of the brain.

A classic experiment which indicated the amazing ability of the brain to rewire itself was carried out by Mriganka Sur and colleagues at MIT in 2000. They rerouted the visual input from the retina to the auditory cortex in newborn ferrets. Amazingly, the auditory cortex was able to process the visual input, and the ferrets could “see” with their auditory cortex.⁷⁶ The “neuroplasticity” of the brain is lucidly described by psychiatrist and psychoanalyst Norman Doidge, in his book *The Brain That Changes Itself*.⁷⁷ Doidge provides an inventory of clinical cases that indicate the brain’s wondrous plasticity and ability to recover from massive lesions by re-inventing neural abilities from scratch, amazingly often in different regions of the brain. The examples range from stroke patients learning to speak again to the remarkable case of a woman born with half a brain that rewired itself to work as a whole so efficiently that, as Doidge comments: “A neurologist would not likely guess, without a brain scan, that a whole hemisphere is missing.”⁷⁸

Further dramatic evidence of the developmental robustness of the language organ was noted by Chomsky:

The language faculty functions in humans even under conditions of severe pathology and deprivation. Children afflicted with Down’s syndrome... who are incapable of many intellectual achievements, nevertheless appear to develop language in something like the normal manner... There are even examples of children who have created a system much like normal language without any experience with language at all—deaf children who have not been exposed to the use of visual symbols but who developed their own species of sign language, a language that has all the essential properties of spoken languages but in a different medium.⁷⁹

Given the evidence that the brain possesses amazing powers of self-regeneration and remodeling and that the generation of linguistic ability during ontogeny is the result of the self-organization of the developing brain, *surely self-organizational phenomena must have also played a crucial if not decisive role in phylogeny*. Alfred Wallace was right: The origin of our intellectual and linguistic abilities involved causal factors in addition to natural selection.

10.9 Summary of This Chapter

A massive consilience of evidence tells against the notion that our novel intellectual abilities and linguistic competence arose from a prolonged evolutionary process, directed by cumulative selection, which *gradually reconfigured* a vast suite of genetic changes in the genome and a corresponding set of neuronal changes in the brain.

First, as pointed out by Wallace, our current intellectual abilities (mathematical, musical, artistic, etc.) could not have possessed any utility on the ancient Pleistocene savanna.

Second, no explanation for why such extraordinary powers should have remained latent for millennia after their origination, 500,000 to 200,000 years ago, has ever been provided.

Third, our linguistic evolution had to occur in a short period of time in small populations in which adaptive mutations were bound to have been very rare, and in which drift would have predominated over selection as the major cause of mutational substitution.

Fourth, there is the discovery that of the very few genes that were under positive selection along the line leading to modern humans, very few if any can be construed as being language genes or having any direct influence on our higher mental abilities.

Finally, there is the fact that in ontogeny, self-organization rather than detailed genetic specification would seem to be the major process responsible for the generation of the language organ.

In short, there are simply no cogent reasons for inferring that language and our higher mental faculties were acquired over hundreds of thousands of generations by gradual cumulative selection of tiny genetic changes in small populations of hunter-gatherers on the plains of Pleistocene Africa. As far as this taxon-defining trait is concerned, everything points to the conclusion of Wallace and to the saltational model of Chomsky: *to emergence, to epigenesis, to self-organization—to internal causal factors as having played a decisive role.*

10.10 Recapitulation of My Argument to This Point

That the gaps cannot be dismissed as inventions of the human mind, merely figments of an anti-evolutionary imagination—an imagination prejudiced by typology, essentialism or creationism—is amply testified by the fact that their existence has been just as firmly acknowledged by the advocates of evolution and continuity. While it may have been the anti-evolutionists who, in perceiving the enormity of the empirical challenge posed by the existence of breaks in the order of nature, coined the phrase “missing links,” it has been the evolutionists... who have sought them with such persistence.

Michael Denton, *Evolution: A Theory in Crisis* (1985), 345.

In *Evolution: A Theory in Crisis*, I argued that where there are “empirical gaps” in the natural order, witnessed in the absence of transitional forms leading to the taxa-defining novelties—feathers, hair, mammary glands, body plans, pentadactyl limb, the flower, and so on *ad infinitum*—it is invariably hard (or impossible) to envisage how they might have been crossed hypothetically in tiny adaptive steps. I further argued that this problem confirms the typological contention that the gaps and the Types they separate are real features of the order of nature and not mere sampling errors. I wrote:

Evolution by natural selection would be established beyond any reasonable doubt, even without empirical evidence of intermediates, if it had been shown that all the great divisions of nature could at least theoretically have been crossed by inventing a really convincing series of hypothetical and fully functional transitional forms.⁸⁰

In the context of the enigma of life’s origin, I wrote:

The failure to give a plausible evolutionary explanation for the origin of life... represents yet another case of a discontinuity where a lack of empirical evidence

of intermediates coincides with [a] great difficulty in providing a plausible hypothetical sequence of transitional forms. It therefore tends to reinforce the possibility that the discontinuities of nature may be much more fundamental than merely the artefactual result of random sampling.⁸¹

This highly suggestive coincidence brings us to the heart of the matter and to the basic contention defended in *Evolution* and re-defended here: *Nature is in fact a fundamental discontinuum of distinct Types and not the functional continuum maintained by Darwinian orthodoxy*. With Rupert Riedl's "hundred thousand" taxa-defining novelties still awaiting Darwinian reduction after two centuries of heroic effort since the foundation of modern biology, this is the only sensible inference that can be made. And when the fantastic invariance of these novelties in so many diverse lineages for hundreds of millions of years is considered in conjunction with the seemingly intractable problem of accounting for their origin in terms of incremental functionalism, the structuralist claim that they represent robust natural forms, intrinsic features of the natural order, is impossible to refuse.

Further reinforcing the deep significance of this universal coincidence are the challenging revelations of evo-devo, most of which came *after* my earlier book was published. Instead of "closing the gaps," evo-devo studies—as witnessed in studies of the development of the feather, the bat's wing, the tetramerous and pentamerous flowers of angiosperms, the endometrial stromal cell, and so forth—provide not the slightest evidence that these novelties came about as a result of gradual cumulative selection to satisfy a long succession of functional constraints.

As I was preparing the final manuscript for this book, I came across two intriguing reports, both of which further undermine Darwinian functionalist claims. The first, which is supportive of the claim that the "gaps" are indeed real and not mere sampling errors, as the "Darwinian propaganda machine" tirelessly proclaims, involves the tympanic ear in terrestrial vertebrates. Briefly, the tympanic ear consists of an outer vibration-receiving membrane (the tympanic membrane), a connecting bone or bones transmitting the vibrations from the tympanic membrane through an air pocket (the middle ear), and a cavity where the vibrations are sensed and transduced into nerve impulses and transmitted to the brain (the inner ear). Fish and primitive amphibians have no middle ear or tympanic membrane, only an inner ear.

For many years, it was assumed that the tympanic ear only originated once in tetrapod phylogeny and that all tympanic ears were homologous. But this turns out not to be the case. As the authors of a recent paper comment: "Tympanic hearing is a true evolutionary novelty that appears to have developed *independently in at least five major tetrapod groups...* in the lines leading to amphibians, turtles, lepidosaurs (lizards and snakes), archosaurs (crocodiles and birds) and mammals."⁸² If the conventional view was correct that evolutionary novelties arise gradually through interminable series of intermediate forms, then surely at least one tym-panic origin would indicate this. But no! None of the five origins of this remarkable adaptive device are led up to via Darwin's "interminable number of intermediate forms."⁸³

The second report comes from a paper published recently in the journal *Evolution* (alluded to in Chapter 5) in which the authors created what they claimed was a "dinosaur

snout” by genetic tampering with the expression of a set of genes involved in the developmental module which generates the beak in a bird. Inhibitors of the gene products involved in beak development caused the chicks in the study to develop a reptilian snout, an apparently genetically engineered atavism. Evolutionary biologists might reasonably see such an experiment as supporting the notion of descent with modification, but it would be very wrong, as always, to conflate evidence for descent with modification with evidence for Darwinism. In fact, as the authors themselves comment on their work:

The abrupt geometric gap between nonbeaked archosaurs and birds and stem birds with beaks may suggest a rapid, comparatively saltational transformation. The difference in ontogenetic trajectories of shape change between nonbeaked forms, in which the premaxilla becomes shorter and broader with time, and beaked forms, in which it becomes longer and narrower, also suggests a discontinuous distinctiveness to the beak.⁸⁴

Only future work can determine just how discontinuous the evolution of the beak actually was, and what role selection might have played, but it seems clear that the *actualization* of the beak only occurred because the basic developmental system of the reptilian snout was pre-figured or pre-adapted for the transformation. Yet again, “internal causal factors” were paramount in the origin of the beak and in the channelling of evolution towards the modern avian Type. As a result of this work, there are now six well-characterized taxa-defining novelties in birds which would appear to have been primarily the result of internal causal factors and not gradual cumulative selection to serve a succession of environmental constraints: (1) the feather follicle; (2) the plumaceous feather with un-branched parallel barbs; (3) the branched pinnate feather; (4) the open pennaceous feather with barbs and barbules; (5) the closed pennaceous feather with interlocking barbules; and now also (6) the beak. In none of these cases is there an adaptive continuum leading to the novelties as would be required by an externalist Darwinian account. Again, “internalism rules.”

Finally, there is the overriding definitional challenge to the Darwinian narrative arising from the fact that many of the taxa-defining homologs and ground plans—such as the pentadactyl limb, angiosperm flower, and the floral formulae of the angiosperm sub-clades—have never been shown to have any specific utility in any *actual* organism in any *actual* environment.

It was this failure to account for structure in terms of adaptive function which was the basis of Owen’s critique of functionalism in *Limbs*. However, the enormity of the challenge this failure posed was lost on me when I wrote my earlier book because of my ardent functionalism. But now I see the likelihood that much of the order of life is in essence a-functional as decisive—the most important challenge to Darwinism by far.

If many of the homologs and ground plans are indeed non-adaptive and *have never served any specific functional end*, the entire Darwinian narrative is rendered a house of cards. Darwinism can be dismissed on this count alone, and all other anti-Darwinian arguments—however cogent—are in essence superfluous.

The enormous advances in knowledge since 1985 have only confirmed my claim in *Evolution* that the Types are distinct and isolated and not led up to via long series of

functional transitional forms as Darwinism demands. On the contrary, the evidence pointed then and points even more emphatically today to discontinuity and to the ultimate Darwinian nightmare—that the gaps were crossed *per saltum* or at least in a series of jumps, a mode of sudden emergence which eliminates any possibility of attributing agency to natural selection, even in those cases where the homolog is clearly adaptive.

In his much-maligned book, *The Material Basis of Evolution*, geneticist Richard Goldschmidt argued that an accumulation of microevolutionary changes could never have summed up to macroevolutionary innovations, and he offered a challenge:

I may challenge the adherents of the strictly Darwinian view, which we are discussing here, to try to explain the evolution of the following features by accumulation and selection of small mutants: hair in mammals, feathers in birds, segmentation of arthropods and vertebrates, the transformation of the gill arches in phylogeny including the aortic arches, muscles, nerves etc.; further, teeth, shells of mollusks, ectoskeletons, compound eyes, blood circulation, alternation of generations, statocysts, ambulacral system of echinoderms, pedicellaria of the same, cnidocysts, poison apparatus of snakes, whale-bone... corresponding examples from plants could be given.⁸⁵

Goldschmidt's challenge has never been met. And we can add to his list the many additional novelties discussed in the previous chapters, and those mentioned in *Evolution: A Theory in Crisis*, including the bacterial flagellum,⁸⁶ and the absolutely unique copulatory organ of the male dragonfly (one of my personal favourites), which is described by Robert Tillyard in his classic, *The Biology of Dragonflies*, as “not homologous with any known organ in the Animal Kingdom; it is not derived from any pre-existing organ; and its origin, therefore, is as complete a mystery as it well could be.”⁸⁷

Altogether, the Darwinian claim that the taxa-defining novelties—and consequently, the Types which they define—have no special place in the natural order and are mere artifactual assemblages of matter—built up bit by bit, by trial and error, to serve various functional constraints—is *without any empirical or rational support*.

Of course, adaptation is ubiquitous in the organic realm—no structuralist ever denied this. Adaptation must be presumed to be responsible for shaping a great deal of organic order. No one would seriously doubt that it was adaptation which shaped the specific forms of tetrapod limbs or the specific forms of insect mouth parts. And adaptation may have played at least *some* role in the actualization of homologs like the bat's wing and even the feather, which are clearly adaptive structures. But there is no evidence even in these cases that it was the sole or even the major player, and there is absolutely no evidence for believing that their actualization was achieved gradually via Darwin's “interminable number of intermediate forms.”⁸⁸

On the evidence available, internal rather than external causation must be presumed to have played a decisive role in the actualization of the great majority of the homologs, whether adaptive or apparently nonadaptive. While Darwin was surely correct that selection played a role in fashioning the beaks of the finches and the patterns imprinted on a peacock's feathers, it is just as surely an “awful stretcher”⁸⁹ (to borrow Darwin's own phrase) to believe that it was primarily selection to serve some functional end that

determined the whorled pattern of the flower, or that led to the origin of the bizarre copulatory organ of the dragonfly, or that produced the arc-shaped gradient in the developing insect limb.

I have now presented what I judge to be decisive arguments against Darwinian evolution. However, in the next two chapters I want to explore two additional points that further undermine the Darwinian account. In Chapter [11](#), I will briefly examine the claim that chance saltations might offer an alternative route to Darwinian gradualism across the divides; and in Chapter [12](#), I will examine the long-term trends in the fossil record which are inconsistent with the Darwinian view of evolution as an undirected process.

After these two chapters, I will present my positive alternative to Darwinian evolution in Chapter [13](#), followed by a wrap-up of my argument in Chapter [14](#).

11. Beyond Chance: *Natura Non Facit Saltum*

Alice laughed. “There’s no use trying,” she said: “one can’t believe impossible things.” “I dare say you haven’t had much practice,” said the Queen. “When I was your age, I always did it for half-an-hour a day. Why, sometimes I’ve believed as many as six impossible things before breakfast.”

Lewis Carroll, *Through the Looking-Glass* (1871), Chapter 5.

If gradual natural selection is powerless to generate the most important biological features in the history of life, as I have argued in previous chapters, then what about relying on chance saltations as an alternative mechanism? As this chapter will explain, the sheer complexity of biological life renders such a proposal incredible. Chance cannot resuscitate the corpse of Darwinian evolution.

More than thirty years ago, I wrote:

It would be an illusion to think that what we are aware of at present is any more than a fraction of the full extent of biological design. In practically every field of fundamental biological research ever-increasing levels of design and complexity are being revealed at an ever-accelerating rate. The credibility of natural selection is weakened, therefore, not only by the perfection we have already glimpsed but by the expectation of further as yet undreamt of depths of ingenuity and complexity.¹

These sentiments have proved remarkably prescient. The complexity revolution has continued—and continues—unabated! A 2010 *Nature* article asks “if there’s a way to make life simpler”² and quotes Jennifer Doudna, a biochemist at the University of California, Berkeley: “It seems like we’re climbing a mountain that keeps getting higher and higher... The more we know, the more we realize there is to know.”³ Many recent papers capture the growing complexity of living systems, particularly at the molecular and cellular level.⁴

Stunning complexity is everywhere in current biology. Even the recruitment of a single gene into a *new gene circuit* is no simple matter, as pointed out in Chapter 7 in the section on ORFan genes. In fact, the mere “turning on” of a gene is accompanied by a vast complex of regulatory mechanisms to ensure the expression of the gene in the right place at the right time and in the right amount. Such controls are obligatory to avoid molecular chaos in the cell. The complex sorts of regulation that apply are indicated in a recent paper on the control of *Hox* gene expression.⁵

What has been discovered at the heart of life is what I have previously termed “the third infinity.”⁶ Whereas the cosmos is an infinity of the very large, and the atom is the infinity of the very small, the organism is the infinity of the very complex. That such an infinity might have come about *in finite time* as a result of any sort of undirected random process seems impossible. Only metaphor can capture the reality now unfolding, for the infinity does indeed beckon through “caverns measureless to man,” to quote from Samuel Coleridge’s famous poem.⁷

The complexity of living systems is so great that there is now an almost universal consensus, as we saw in the discussion of ORFan genes, that the simplest of all biological novelties—a single functional gene sequence—cannot come about by chance mutations in a DNA sequence. And if an individual gene sequence is far too complex to be produced by chance, then the sudden origination of a morphological novelty like a feather, a limb, or even such a comparatively simple novelty as an enucleate red cell—all novelties vastly more complex than an individual functional gene sequence—is by any common-sense judgment far beyond the reach of any sort of undirected “chance” saltation. Only if nature were specifically pre-arranged for the actualization of such novelties would it be conceivable that they could originate in saltational jumps.

According to Fred Hoyle’s famous calculation,⁸ the probability of the evolution of cellular life by chance is about one in $10^{40,000}$. He illustrated the probability thus:

A junkyard contains all the bits and pieces of a Boeing 747, dismembered and in disarray. A whirlwind happens to blow through the yard. What is the chance that after its passage a fully assembled 747, ready to fly, will be found standing there? So small as to be negligible, even if a tornado were to blow through enough junkyards to fill the whole Universe.⁹

Everyone—Darwin, Mayr, Fisher, Dawkins, Dennett, Hoyle, and creationists—agrees that the probability of such a sudden assembly in biological contexts is close to zero. And as we saw, all the authors cited above in the section on ORFan genes reject the notion that a single functional gene sequence could emerge by chance.

As Darwin bluntly put it in the *Origin*:

He who believes that some ancient form was transformed suddenly through an internal force or tendency... will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced; and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of an explanation... To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of Science.¹⁰

Darwin’s skepticism regarding the possibility of complex organic systems coming into existence by chance saltation is almost certainly justified. His views were reiterated by one of the leading makers of the Modern Synthesis, Ronald Fisher. In his *Genetical Theory of Natural Selection*, Fisher comments: “For [mutational changes] the chance of [adaptive] improvement diminishes progressively, becoming zero, or at least negligible, for changes of a sufficiently pronounced character.”¹¹ Fisher illustrates this in a famous graph¹² and with an analogy:

The conformity of these statistical requirements with common experience will be perceived by comparison with the mechanical adaptation of an instrument, such as a microscope, when adjusted for distinct vision. If we imagine a derangement of the system by moving a little each of the lenses, either longitudinally or transversely, or by twisting through an angle, by altering the refractive index and transparency of the different components, or the curvature, or the polish of the interfaces, it is sufficiently obvious that any large

derangement will have a very small probability of improving the adjustment.¹³

Fisher concludes:

If therefore an organism be really in any high degree adapted to the place it fills in its environment, this adaptation will be constantly menaced by any undirected agencies liable to cause changes to either party in the adaptation... [Consider the case of large mutations.] A considerable number of such mutations have now been observed, and these are, I believe, without exception, either definitely pathological (most often lethal) in their effects, or with high probability to be regarded as deleterious in the wild state.¹⁴

In their rejection of saltation, Darwin, Fisher, the makers of the Synthesis, Dawkins, and the others are surely right. Undirected change cannot build complex novelties of the sort that define the taxa of the natural system *in sudden large jumps*. Small wonder that, as Massimo Pigliucci comments, “ever since Goldschmidt (1940) professed dissatisfaction with the MS’s [Modern Synthesis’s] ability to explain variation across species, his ‘hopeful monsters’ have repeatedly reared their ugly heads and have consistently been beaten back by defenders of the orthodoxy.”¹⁵

As we saw in Chapter 2, cumulative selection *can* be the causal agency responsible for the creation of a complex biological novelty if the novelty can be reached via a long sequence of transitional adaptive forms. But if the novelty cannot be actualized in this way, either because it is obviously a non-adaptive *Bauplan* (like the tetrapod limb, or the angiosperm flower) or because no adaptive intermediates can be conceived of (as in the case of adaptations like the bat’s wing or human language), it is no use turning to undirected chance saltations or “hopeful monsters” as a way of making the leap, as some authors do.¹⁶ If cumulative selection has no functional continuums to traverse the gaps, or if a novelty appears to be a non-adaptive ground plan, then it could only have been actualized by some directive agency other than cumulative selection. Either the “jump” was, as mentioned above, already prefigured into the biology of the ancestral form and its actualization due to internal causal factors according to a structuralist “laws of form” framework (Owen’s “nomo-genesis”), or it came about as the result of special creation.

The sheer bankruptcy of the claim that novelties which are not led up to via empirically known incremental functional sequences might have been found by “chance” macromutations which “just happened to put together” complex structures like a mammalian hair, a diaphragm, a bat’s wing, a branched bipinnate feather, etc., is only too obvious. Evolutionary biology is clearly a theory in deep crisis if evolutionary biologists have to enter Darwin’s realm of miracle to account for the emergence of evolutionary novelties that are not led up via Darwin’s long chain of “innumerable transitional forms.”¹⁷

12. Fossils: Long-Term Non-Adaptive Trends

Natural selection acts exclusively by the preservation and accumulation of variations, which are beneficial under the organic and inorganic conditions to which each creature is exposed at all periods of life. The ultimate result is that each creature tends to become more and more improved in relation to its conditions.

Charles Darwin, *On the Origin of Species* (1872), Chapter 4.

Reinforcing the consilience of evidence against Darwin and providing further evidence for the structuralist claim that internal causal factors have played a critical role in evolution are the many long-term “orthogenetic” trends in the fossil record. These trends manifest themselves as continuous, unidirectional change in all the successive members of particular lineages, sometimes over millions or hundreds of millions of years. Constant directional change of this sort is inexplicable in terms of neo-Darwinism because organisms, according to Darwinian theory, are shaped only by cumulative selection for day-to-day or immediate utility; to explain long-term unidirectional trends in strictly Darwinian terms would necessitate the highly implausible postulate of *constant selective constraints* operating on all the successive and often diverse members of the lineage over millions of years in diverse environments.

Consider a simple hypothetical example. Imagine a lineage of organisms stretching over millions of years, some aquatic, some terrestrial, some airborne, some herbivorous, some carnivorous, etc., where the size of successive members of the lineage continually decreased, from elephant-sized to mouse-sized by the end of the lineage. Given the extreme diversity of the members of the lineage and the very different environmental constraints to which they would be inevitably subject, the only explanation would be to assume that the reduction was caused by some internal non-adaptive (i.e., orthogenetic¹) causal factor, which had acted continuously during the entire history of the lineage. Such a trend could be properly termed “non-adaptive.” Of course, most actual ortho-genetic trends do not involve such a simple parameter as size, but rather involve much more complex types of change in particular organ systems or morphological motifs.

The existence of long-term trends in the fossil record was one of the reasons why many leading paleontologists in the century after Darwin—including such luminaries as Henry Fairfield Osborn and Edward Drinker Cope—subscribed to some version of orthogenesis, maintaining that in many instances long-term evolutionary change is directed by internal causal factors which have no obvious connection with day-to-day environmental fitness or functional necessities.² Yet it was not just paleontologists who subscribed to orthogenetic notions during this period. Leo Berg listed several authors from other disciplines, including Theodor Eimer, John C. Willis, Henry Leo Przibram, and Curtis O. Whitman.³ Even Thomas Huxley was not averse to the idea that long-term evolutionary changes might be directed by internal non-adaptive constraints. Pointing out that variation may not occur in all directions, he commented: “A whale does not tend to vary in the direction of feathers, nor a bird in the direction of developing whalebone.”⁴

Being deeply anti-Darwinian in spirit, orthogenesis has fallen out of favor today and

is often caricatured as involving long-term trends towards maladaptive ends leading to the eventual extinction of the lineage. Classic cases often cited include the enlarging antlers of the Irish Elk, the large canines of the saber-toothed cats, and the overcoiling of one of the shells in the oyster *Gryphaea* which caused self-strangulation.⁵

Intriguingly, both Julian Huxley and J. B. S. Haldane—two of the makers of the neo-Darwinian synthesis—accepted this interpretation of the overcoiling of *Gryphaea*.⁶

Whether the fossil record documents any genuinely long-term trends towards maladaptive ends is controversial. But it does document long-term, *unidirectional* trends that appear to have no immediate adaptive utility to the successive species in the lineage concerned. Such trends suggest strongly that macroevolution does indeed involve, as *evo-devo* also implies, internal causal factors in addition to cumulative selection for functional ends.⁷

12.1 The Reduction of the Gametophyte Generation in Land Plants

One of the most stunning cases of an apparently long-term non-adaptive trend is the so-called “reduction of the gametophyte generation” in land plants. This is such an extraordinary phenomenon that it is worth considering in some detail. The challenge it poses to any functionalist interpretation of the evolution of plants is self-evident.

The temporal succession of land plants started in the Ordovician period some 450 million years ago with the appearance of simple nonvascular plants (without lignified internal transport mechanisms, roots, stems, or true leaves)—the bryophytes, including the mosses and liver-worts. These were followed by the emergence of the various classes of vascular plants, including (1) club mosses, horsetails, and ferns (which lacked seeds but possessed advanced water-transport systems and woody trunks, permitting growth to heights of fifty meters in the Carboniferous forests), and (2) the true seed-bearers, first the familiar conifers (gymnosperms), and then the flowering plants (angiosperms). Successive forms show increased development of water-transport mechanisms, the development of woody trunks, the rise of complex leaves, and advances in reproduction involving the evolution of the seed and (in the case of the flowering plants) the fruit.⁸ The evidence suggests that each “more complex” group arose from the most complex pre-existing group at the time.⁹

While many of the new features which emerged during this succession, namely water-transport systems, leaves, seeds, etc. can be viewed as adaptive, at the same time a mysterious trend was occurring in the reproductive cycle which has never been satisfactorily accounted for in adaptive terms, and which continued for 400 million years.

To understand the enigmatic nature of this trend—the reduction of the gametophyte generation—recall that in all land plants from mosses to angiosperms (flowering plants) the reproductive cycle is divided into two multicellular stages: the sporophyte phase (the diploid generation with the full complement of chromosomes, $2n$) and the gametophyte phase (the haploid generation with half the full complement of chromosomes, $1n$).¹⁰ In flowering plants, the sporophyte ($2n$) is the main body of the plant (comprising the branches, leaves, flowers etc.), while in the mosses the gametophyte ($1n$) phase forms the main and conspicuous part of the plant. The sporophyte in all plants, from mosses through ferns and gymnosperms to angiosperms, produces the sex cells or gametes (by a reduction

division or meiosis). And in all plants the gametes undergo ordinary cell divisions, producing a multicellular gametophyte, which eventually gives rise to the gametes that fuse to form a fertilized egg cell, which grows into the sporophyte.¹¹

But although *all* terrestrial plants consist of these two multi-cellular stages, in the earliest plants the haploid phase or gametophyte formed the main body of the plant and the sporophyte was a mere reproductive appendage, as in extant mosses where what we see—the green fleshy fronds—is the gametophyte (composed of haploid cells, $1n$). But in the case of an angiosperm or flowering plant what we see, i.e., the stems, leaves, and flowers, make up the sporophyte (composed of diploid cells, $2n$). As we move from mosses to horsetails to ferns to conifers to flowering plants, the gametophyte becomes reduced, step by step, from the main part of the plant in the mosses to a small but still independent part of the plant in the ferns to only a handful of the cells in the angiosperms.¹² Leo Berg remarks:

We may thus trace the entire process of reduction of the gametophyte, commencing with its flourishing condition in mosses, and proceeding with its gradual decline in the Pteridophyta [ferns], until we come to its complete disappearance in gymnosperms and its final replacement by the sporophyte in angiosperms. A definite course of evolution is here strikingly exemplified.¹³

Berg is surely right. To account for this trend in terms of incremental selection of day-to-day variants in a population of plants is simply to defy reason. One would have to suppose that over a period of 400 million years, in plants as diverse as lycopods, tree ferns, redwoods, and Australian eucalypts, the survival value to individual plants in a population was in some way enhanced by the pull of this mysterious reduction. But what improvement in reproductive fitness could account for such an abstract and mysterious trend over 400 million years in such vastly different plant types? There is no commonality of structure, environment, or function which unites all these diverse plants—fir trees, mosses, apple trees, tree ferns, and so forth—which might have imposed this remarkable 400-million-year trend on their evolution. Moreover, the reduction is by no means gradual and continuous, but occurs in jumps from ferns to gymnosperms to angiosperms, which makes the trend even more mysterious—and even more difficult to account for in terms of incremental functionalism. Berg makes the same point: “A definite course of evolution, which may be traced from the Pteridophyta [the ferns] through gymnosperms to the angiosperms, is thus manifested in various genetic branches, thereby adding weight to the importance of the orthogenetic process.”¹⁴

Darwinian evolution, with its short-term vision, tests only the immediate adaptive value of mutations, and is impotent to impose such an extraordinary trend on the major plant lineages for 400 million years. To my knowledge, no convincing explanation based on Darwinian assumptions has ever been given for this trend. Some causal factor other than selection for immediate environmental fitness must surely have been involved throughout.

12.2 The Reduction of the Aortic Arches

Another long-term trend that is difficult to account for in terms of a purely adaptive narrative is the reduction of the aortic arches, which can be followed during the course of

chordate evolution from amphioxus via fishes to mammals and birds. The aortic arches are a series of paired blood vessels, which in primitive vertebrates and fish lead from the ventral aorta via the gills to the dorsal aorta, which then carries the aerated blood to the rest of the body.

The primitive chordate amphioxus, a simple fish-like organism about ten centimeters long that is considered to be close to the vertebrate ancestor, has over fifty pairs of arches.¹⁵

The next most advanced chordates are the jawless fishes such as the extant hagfishes and lampreys, which have up to fifteen pairs of arches.¹⁶ In jawed fishes, including all familiar forms of bony fish and sharks, the number of aortic arches never exceeds six in either the embryo or adult form.¹⁷ In adult sharks the number is six, although arch one is much reduced. In lungfish, it is five (two, three, four, five, and six); in most familiar bony fishes (Teleosts) it is four (three, four, five, and six). In terrestrial vertebrates, it is never more than four. In newts and salamanders (Urodela), it is four (three, four, five, and six), while in frogs (Anura) it is three (three, four, and six). In lizards, it is also three (three, four, and six).¹⁸ In adult birds and mammals, it is in effect two-and-a-half. This is because in mammals and birds, only one branch of the fourth arch is conserved in the adult. In mammals, the left branch of the fourth arch forms the aorta, which curves to the left from the heart; in birds, the right branch of the fourth arch forms the aorta, which curves to the right from the heart.

Thus, we can trace the reduction in the aortic arches as a gradual and persistent phenomenon throughout 500 million years of chordate phylogeny, starting with fifty and ending up with two-and-a-half. Although the loss of arches can be correlated in some instances with adaptive changes (associated, for example, with the transition from water to air breathing and with an increasingly advanced cardiovascular system), there are puzzling aspects which are not easy to explain in terms of adaptation. For example, what adaptive factors led from many arches to six in primitive vertebrates? What limited the number of arches in all subsequent vertebrates to six? What factors were responsible for the parallel reduction in different lineages? In the lineage leading from primitive bony fish to the modern teleosts and in the lineage leading from primitive bony fish to newts and salamanders—two very different lineages subject to the different constraints of water and air breathing—the second arch (two) has been lost in parallel, resulting in both groups having the same aortic formula (three, four, five, and six). Again, in the lineage leading from stem reptiles to birds and in the lineage leading from stem reptiles to mammals, the fifth arch has been lost in parallel in both lines. Yet again, in a quite different lineage, the one leading from stem amphibians to frogs, the fifth arch has also been lost. *So in three tetrapod lineages adapted to very different lifestyles and subject to very different environmental pressures, the same arch (five) has been lost.*

Additionally, what selection pressures might have led to the two higher amniote lineages retaining in one case (mammals) the left branch and in the other case (birds) the right branch of the fourth aortic arch?

As Berg commented on the reduction of the arches: “In this case also [as with the reduction of the gametophyte in plants] a determined direction in evolution is made strikingly evident: what is especially deserving of notice is the identical result reached by

birds and mammals in the development of the arches in various ways and quite independently.”¹⁹

In passing, it is worth noting that both birds and mammals have evolved—completely independently—many similar organ systems, including a four-chambered heart with similar sinu-auricular and auricular-ventricular nodes through which the nervous stimulation is distributed to the heart muscle. The kidneys of birds and mammals contain a unique device for concentrating urine called the loop of Henle, which must have evolved independently in both groups.²⁰ Most remarkable of all is the similarity between the structure of the cochlear and the organ of Corti in the ears of both groups.²¹ It is hard to avoid the conclusion that internal causal factors played an important role in drawing the evolution of these organ systems to such similar ends.

In sum, what makes the deduction to causal factors beyond cumulative selection so convincing is that the individual steps which accompanied the reduction—the loss, for instance, of a particular aortic arch in the three different tetrapod lineages—cannot easily be accounted for in terms of incremental functionalism. So both the grand trend (over 500 million years) and the loss in a particular lineage of a specific aortic arch are incapable of simple reduction to Darwinian functionalism.

12.3 The Reduction of the Forelimbs in Therapods

Another intriguing trend which provides evidence of additional, non-Darwinian processes driving long-term evolutionary change is the gradual reduction of the forelimbs in various lineages of theropod dinosaurs,²² leading eventually, over the course of some 200 million years, to the bizarre reduced limbs of huge predatory dinosaurs such as the tyrannosaurids and related groups of “advanced therapods.” In one such group, the Abelisauridae, the forelimbs are essentially vestigial, lacking even phalanges and only protruding from the body a few inches (on a carnivore fifteen meters long): “No wrist bones existed, with the four palm bones (metacarpals) attaching directly to the forearm. There were no finger bones on the first or fourth digits, only one on the second digit and two on the third digit. These two external fingers were extremely short and immobile”²³ [internal references removed].

The gradual reduction in so many diverse theropod lineages, resulting in a vestigial and useless appendage, is obviously hard to put down to cumulative selection. What obscure adaptive end was served in the Abelisaurids by the single phalanx on the second digit and the two phalanges on the third digit? Echoes of Bateson’s absurdities again?

Another intriguing long-term trend within the dinosaurs was the progressive reduction and loss of digits: First digit five was lost, then digit four, over hundreds of millions of years of evolution in diverse types. This reduction is also seen in the lineage that eventually led to birds.²⁴

12.4 The Reduction of the Post-Dentary Bones in Synapsids (Mammal-like Reptiles)

Another classic case of a long-term trend that is hard to explain in terms of adaptation, i.e., as being imposed by a constant adaptive constraint, is the reduction of the post-dentary bones in the jaws of successive clades of mammal-like reptiles (the ancestors of the

mammals) over approximately 150 million years²⁵ (see Figure 12-1 below). This reduction occurred in parallel in several different advanced synapsid lineages.²⁶ (In fact, the synapsids exhibited a number of long-term trends in addition to the reduction of the post-dentary bones, which also occurred in parallel in different lineages.²⁷)

Reptiles have four main bones in the lower jaw—the dentary, articular, angular, and surangular—while mammals have only one, the dentary. In reptiles, the jaw joint is composed of the quadrate, which is part of the skull, and the articular, which is part of the jaw, while in mammals it is formed from the squamosal (part of the skull) and the dentary.²⁸ In successive groups of synapsids, the articular and angular were successively reduced until they were tiny post-dentary bones (see Figure 12-1), while the surangular was gradually absorbed into the dentary. As the reduction occurred, a second joint originated between the squamosal and the dentary in several synapsid lines (Figure 12-1).²⁹ The two bones rendered “redundant” after the evolution of the second joint, the articular and the quadrate, were incorporated into the mammalian ear as the malleus and incus respectively, forming two of the chain of three bones leading from the eardrum to the inner ear³⁰ (see also the discussion of ear evolution in Chapter 6, Sec. 6.2). Moreover, recent studies suggest that the definitive mammalian middle ear was also acquired independently and in parallel in several different lineages of early mammals.³¹ There is no doubt that parallel evolutionary trends for which adaptive scenarios are hard to envisage are marked in the synapsids. In a detailed analysis of these trends in the advanced synapsids, Hans-Dieter Sues comments:

Parallelism is a common phenomenon in phyletic evolution. El-dredge goes even further, stating that “parallelism turns out to be a *far more common evolutionary phenomenon than even most of its more ardent aficionados had thought.*” Alberch has pointed out in an elegant review that the production of morphological novelties is constrained by developmental programmes. Characters can be viewed as end products of developmental pathways; selection is responsible for the “fine tuning” of adaptations within limits defined by intrinsic epi-genetic properties. Such shared epigenetic programmes can result in parallelisms in particular character complexes among related lineages... Extensive parallel evolution in features of both the skull and the postcranial skeleton is evident among advanced synapsids, regardless of the preferred hypotheses of tritylodontid relationships.³²

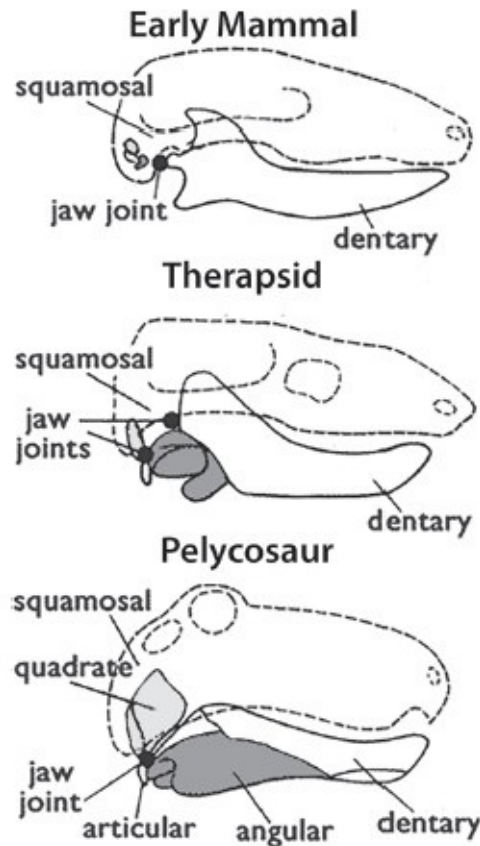


Figure 12-1. Jaw Evolution. The reptile-to-mammal jaw transition, with the Therapsid showing a double jaw joint.”

An adaptive scenario to account for the reduction of the post-dentary bones is hard to envisage. It is hard to convince oneself that the reduction was for enhanced hearing (to assist in transmitting sound vibration to the middle ear) as some authors propose. Even if this explanation might work for the final stages when the post-dentary bones were already very small, it cannot explain the earlier stages of the reduction when the bones were still substantial parts of the jaw. Whatever the reason, the reduction and ultimate loss could hardly have been an adaptation to *strengthen the lower jaw* for some obscure purpose. Species with powerful bites, such as extant crocodiles and the iconic *Tyrannosaurus rex* (which had the most powerful bite force of any extant or extinct terrestrial predator³³), need very strong lower jaws able to sustain the enormous stresses associated with such powerful bites, and have “typical” reptile jaws composed of four different bones. Again, it is hard to see how the reduction could have been driven by the evolution of mammalian mastication and dentition, as it is hard to see how such tiny bones could have played any relevant adaptive role. Moreover, the reduction appears to have started early in synapsid evolution, before the development of “mammal-like mastication.”

12.5 The Reduction of Whale Hind Limbs

The reduction of the hind limb of extant cetaceans is another example where a non-adaptive trend appears to have shaped an evolutionary transition. At the Dover trial, Kevin Padian described the transitional sequence starting with *Ambulocetus*:

Ambulocetis means “walking whale”... It still has legs, and... it’s perfectly OK getting around on land, but... the limbs are large and paddle-like... the hands and feet are clearly already being broadened and are apparently of some use to the animal in getting around in the water... The next slide shows you

protocetids, which are ancient whale relatives that are a little bit closer [to modern whales than *Ambulocetus* is]. Even though these animals are quite aquatic and have a lot of whale features, they still have ankle bones that are very much like the ankle bones in the hoofed mammals from which they evolved... These animals are spending more and more time in water, but they can still deal okay [with land]... [In the] basilosaurids, the next step toward living whales...³⁴ the hind limb bones are now not just decoupled from the back bone; they've become extremely reduced... [but] that pulley-shaped bone... is the ankle... [it] is still like the ankle of a terrestrial animal, a hoofed mammal, from which they evolved, even though this animal couldn't any more walk on land than it could fly. So what we are seeing here is the progression of features more and more whale-like... the final thing we have here is the living cetacean [modern whale].³⁵

But can we infer that the causal mechanism of the successive modifications was cumulative selection alone, or were other factors also involved? The succession of whale ancestors do indeed exhibit increasing adaptations for marine life and gradual diminishing of the size of the hind limbs. But was the jump between *Ambulocetus* and *Protocetus* and that between *Protocetus* and *Basilosaurus* the result of gradual cumulative selection? Some argue that these great morphological changes appeared so rapidly in the fossil record (within less than 10 million years) that they could not possibly have arisen and been fixed by Darwinian selection.³⁶ One aspect of the transition is certainly hard to account for in adaptive terms: the final stages in the reduction of the hind limbs from tiny but almost complete hind limbs to mere vestigial remnants in most modern whales.³⁷ These final stages of their elimination, when the reduced limbs were entirely encased in the immensity of the whale's body, are obviously problematical. As Gould comments:

What conceivable pressure of natural selection could account for gradual stages in the disappearance of a *functionless organ*—for loss of function should remove a structure from the domain of selection entirely, and knowledge about an eventually adaptive state could not be invoked to guide an explanation for intermediary states along such a functionless path.³⁸

The reduction of whale hind limbs troubled the great Darwinist August Weismann, who debated the issue with Herbert Spencer in the 1890s. As Spencer points out in his correspondence, a Greenland Right Whale, weighing 44,800 pounds, has a femur which weighs only three and a half ounces, and a Razorback (Finback) weighing 56,000 pounds, has a femur of one ounce, “so that these vanishing remnants of hind limbs weighed but 1/896,000 part of the animal.”³⁹ Weismann was forced to concede the point:

To use Herbert Spencer's striking illustration, how could the balance between life and death, in the case of a colossus like the Greenland whale, be turned one way or another by the difference of a few inches in the length of the hind-leg... Further reduction to their modern state of great degeneration and absolute concealment within the flesh of the animal cannot be referred even to negative selection.⁴⁰

Moreover, many large marine vertebrates retained their hind limbs: ichthyosaurs, plesiosaurs, and of course modern seals, which are almost as well-suited for life in the

oceans as whales but have retained their hind limbs for tens of millions of years, a period about as long as that covering the entire evolution of the whales. If seals have retained their hind limbs for adaptive reasons, why did the whales lose theirs? A host of additional questions are raised when the morphological changes are considered in detail. One intriguing detail—the teeth of one group of primitive whales, the basilosaurids, are fairly typical of primitive mammals and very seal-like, while the teeth of dolphins and killer whales are unique in mammals, simple pegs. Was the change adaptive? Seals are able to catch fish efficiently with standard mammalian teeth and presumably so did the basilosaurids.

It is no wonder that so many paleontologists interpreted such trends as examples of orthogenesis. Henry Fairfield Osborn, one the giants of American paleontology, expressly rejected the pan-adaptationist paradigm. One phenomenon he alluded to is the peculiar occurrence in diverse mammalian lines of recurrent patterns of dental cusps. These are the small tubercles on the upper surface of the molars and premolars in mammals. Osborn's studies convinced him that there were very striking non-adaptive trends in the evolution of cusp patterns. And the evidence is certainly convincing, as anyone who consults Osborn's work will concur.⁴¹ He wrote:

My study of teeth in a great many [groups] of mammalia in past times has convinced me that there are fundamental predispositions to vary in certain directions; that the evolution of teeth is marked out beforehand by hereditary influences which extend back hundreds of thousands of years. These predispositions are aroused under certain exciting causes and the progress of tooth development takes a certain form converting into actuality what has hitherto been potentiality... Philosophically, predeterminate variation and evolution brings us upon dangerous ground. If all that is involved in the Tertiary molar tooth is included in a latent or potential form in the Cretaceous molar tooth, we are nearing the *emboitement* hypothesis of Bonnet or the archetype of Owen and Oken.⁴²

The literature on trends is vast, but now largely ignored because of its anti-Darwinian ethos.⁴³ However, there is no doubt that what appear to be non-adaptive trends do occur in the fossil record, and these undermine further the Darwinian claim that natural selection was the major causal agency of macroevolution. Many years ago Osborn, in characteristic regal style, summed up the situation, and no discoveries since have materially challenged his verdict:

In all the research since 1869 on the transformations observed in successive phyletic series no evidence whatsoever, to my knowledge, has been brought forward by any paleontologist, either of the vertebrated or invertebrated animals, that the fit originates by selection from the *fortuitous*.⁴⁴

Osborn continued in a strikingly structuralist vein:

As in the domain of inorganic nature, so in the domain of organic nature fortuity is wanting, and the fit originates... through laws which are in the main similar to growth—laws the modes of which we see and measure, the causes of which we do not and may never understand, but nevertheless laws and not fortuities or

chance happenings.⁴⁵

12.6 Summary

The existence of long-term trends in the history of life irreducible to any credible functionalist explanation represents another important strand in the consilience of structuralist evidence against Darwinian functionalism presented in this book, evidence showing that the functionalist paradigm cannot in itself provide a comprehensive explanation for the development of life on earth. Causal factors beyond selection—including the developmental constraints now being elucidated by researchers in evo-devo—must have been involved. Indeed, many of the trends can be looked on as providing powerful support for the new evo-devo “developmental constraints paradigm” discussed in Chapter 5. Admittedly, in the case of some of the trends, including the reduction of the gametophyte generation and the gradual loss of aortic arches in vertebrates, it is hard to envisage what developmental constraints might have brought them about. But whatever causal factors were responsible, the trends themselves provide an obvious challenge to Darwinian panadaptationism.

This brings us to the final section of this book, in which I consider the structuralist alternative to Darwinian functionalism—the traditional typological notion of life’s basic forms as built into nature, the result of the long-sought-after “laws of biological form”—and show that it is supported not only by the failure of Darwinian functionalism, i.e., by default, but also by another consilience of evidence, one arising from many recent advances in various fields. These advances are pointing back to the nineteenth century, to Owen, to laws of form, and to the reaffirmation of the reality of the Type. And it is not only advances in biology, but also advances in cosmology, which have revealed the universe to be fine-tuned for life on earth.

13. Typology Redux

“The vague and in some respects false analogies... which have been advanced in favour of this [saltational] view, such as the sudden crystallisation of inorganic substances, or the falling of a faceted spheroid from one facet to another, hardly deserve consideration.”

Charles Darwin, *On the Origin of Species* (1872), Chapter 7.

As Darwin himself said in a celebrated letter to Henry Fawcett, “All observation must be for or against some view if it is to be of any service.”¹ Given the fading plausibility of the neo-Darwinian worldview, this is perhaps a propitious time to mount a defense of the structuralist/typological view. It is propitious also because a number of recent developments provide novel support for the pre-Darwinian structuralist belief that much organic order is the result of intrinsic physical properties of living systems and that the Types are, as Geoffroy² and Owen³ and many other nineteenth-century biologists conceived of them, integral parts of nature.

13.1 The Fitness of the Laws of Nature for Life on Earth

In the Darwinian view, life is an artifactual thing, something apart from nature, its constituent bio-forms mere “contingent assemblages,” artifacts of deep time and chance.⁴ This view is surely one of the strangest inferences in the history of human thought, and an inference for which there never was the slightest rational justification. There are few other examples in science of a cultic belief that represents, in Thomas Nagel’s words, “[such] a heroic triumph of ideological theory over common sense.”⁵ Indeed, from Aristotle down, throughout the medieval period, right up to the seventeenth century, life was always conceived to be an integral part of nature, and its constituent forms—substantial forms—basic components of the world-order. Aristotle conceived of these as active agents in nature, molding the forms of organisms and, through their collective activities, the overall pattern of life on earth.⁶

As Jonathan Lear comments regarding Aristotle’s conception of forms:

Since the seventeenth century Western science has moved steadily away from conceiving forms as part of the basic fabric of the universe... In Aristotle’s world, forms... occupy a fundamental ontological position: *They are among the basic things that are.*⁷

After being in the cold for most of the past 150 years, overshadowed by the “cult of the artifact,” the traditional notion that life is an integral part of the natural order has found renewed support in the revelation of twentieth-century physics and cosmology that the laws of nature are uniquely fine-tuned to a remarkable degree to generate environmental conditions ideal for life as it exists on earth.

The twentieth-century cosmological evidence that the universe is fine-tuned for life is based on the observation that if the various fundamental forces and constants which determine the structure of the cosmos and the properties of its constituents did not have precisely the values they do, there would be no stars, no supernovae, no planets, no atoms, and certainly no life.⁸ As Paul Davies summarizes:

The numerical values that nature has assigned to the fundamental constants, such as the charge on the electron, the mass of the proton, and the Newtonian gravitational constant, may be mysterious, but they are crucially relevant to the structure of the universe that we perceive. As more and more physical systems, from nuclei to galaxies, have become better understood, scientists have begun to realize that many characteristics of these systems are remarkably sensitive to the precise values of the fundamental constants. Had nature opted for a slightly different set of numbers, the world would be a very different place. Probably we would not be here to see it.⁹

On the fine-tuning necessary to generate carbon and the higher elements in the stars, Fred Hoyle famously commented: “A commonsense interpretation of the facts suggests that a superintellect has monkeyed with physics, *as well as with chemistry and biology*, and that there are no blind forces worth speaking about in nature.”¹⁰ [emphasis added] Surely Hoyle was right in thinking that the fine-tuning would extend to the laws of chemistry and biology. If the laws of nature are, for whatever reason, fine-tuned to generate environmental conditions ideally suited to the forms of life that exist on earth, so fine-tuned that, as Davies confesses, “the impression of design is overwhelming,”¹¹ it certainly is not so outrageous to envisage that they might be also biologically fine-tuned to generate the grand hierarchy of forms themselves.

Even before twentieth-century cosmology delivered its verdict, clear evidence that nature is uniquely fit for life as it exists on earth had already come to light in the late nineteenth and early twentieth centuries as a result of advances in organic chemistry, biochemistry, and physiology. This evidence was assessed and reviewed by Alfred Russel Wallace in *The World of Life* in 1910 and by Lawrence Henderson in his great classic *The Fitness of the Environment* in 1913. In the latter work, Henderson argued that carbon-based life as it exists on earth depends critically on a unique mutual synergistic fitness in the properties of the carbon atom, organic compounds, water, carbon dioxide, and oxygen to assemble complex chemical systems exhibiting the properties we associate with life.

The extraordinary unique fitness of nature for carbon-based life described in Henderson’s *Fitness* implies that at least the basic biochemical design of life is immanent in the properties of matter and not an artifact of time and chance as Darwinism implies. Further confirmation of the unique chemical fitness of the cosmos for carbon-based life has come from the recent discovery of a vast and growing inventory of organic compounds in space, including some of the key monomers used in the building of the proteins and nucleic acid polymers in extant life on earth.¹² The evidence that the cosmos is uniquely fit for carbon-based life as it exists on earth (including advanced forms utilizing oxidation as an energy source) is now so compelling that in searching for extraterrestrial life, scientists at NASA “follow the water”¹³ and look for oxygen in the atmospheres of extrasolar planets as a signature of life.¹⁴

The discovery that the cosmos is fine-tuned for life provides powerful circumstantial support for the “laws of form” biology and the notion that life’s basic designs—the taxadefining novelties, *Bauplans*, etc.—are immanent in the world-order. If nature is so fine-tuned for life’s environment, surely the fine-tuning will also extend to the generative arena and include a set of laws of form, geared to actualize the forms of life on earth. The

extrapolation is intriguing and very hard to resist. It is particularly hard to resist considering that the fitness of the cosmic, chemical, and physiological environment for life as it exists on earth does not stop with simple microbial life. It extends even to higher organisms like ourselves.¹⁵ Such an extrapolation would bring us very close to the nineteenth-century conception of life as an integral part of nature and with the notion that the main taxa are invariant universals analogous to atoms or crystals determined by laws of form.

One of the most curious aspects of the almost universal acknowledgement that the cosmos is uniquely fine-tuned specifically for carbon-based life is the failure to take this next logical step and infer that nature may be also fine-tuned for the origin and actualization of the basic forms of carbon-based life which characterize life on earth. *Indeed, I would argue that this failure is one of the most striking failures of the human imagination in recent scientific history.* Despite the eulogies of Paul Davies, George Barrow, Frank Tipler, Martin Rees, John Gribbin, and Roger Penrose on the fitness of nature for life, none of them is prepared to take the next logical step to nomogenesis (evolution by law) and the notion of “laws of biological form.” This failure is all the more striking when it is also widely conceded by many of these same authors that Darwinian explanations have failed in certain key areas, such as the origin of life.¹⁶

There is no doubt that cosmological fine-tuning for life as it exists on earth provides a very powerful line of circumstantial evidence, drawn ironically from *outside* the biological sciences, for a return to a structuralist biology and the notion that life’s origin and evolution were built into the order of nature from the moment of the “big bang.”

13.2 The Epigenetic Revolution

If the laws of nature are indeed fine-tuned for the generation of the Types, as an extension of the cosmological fine-tuning would imply, and if the homologs are indeed a set of natural forms—“among the basic things that are”¹⁷—and immanent in nature, then we should expect that they should arise by analogy with inorganic forms, spontaneously and “unbidden,” unspecified in anything like a genetic blueprint. In both phylogeny and ontogeny, the homologs should arise on structuralist principles from *the self-organization of particular categories of matter*. Just as a crystal of common salt arises when a solution of sodium and chlo-ride ions evaporates, a snow crystal forms when water freezes, or a new atom arises when two nuclei collide and fuse in a stellar interior, so the basic homologs or Types (the “atoms” of biology) should arise, from the cellular to the organismic level, from the self-organizing properties of particular classes of matter—more specifically, of particular classes of biomatter.

Moreover, in the inanimate domain, order that arises from the self-organization of matter is often termed “emergent.”¹⁸ The classical example is water. No matter how exhaustively its two constituents—hydrogen and oxygen—are analyzed, the physical and chemical properties of water cannot be predicted and are strictly emergent; they arise mysteriously out of the self-organization of matter. If the basic forms of life are also natural forms determined by laws of form and ultimately the properties of matter, *their ontogeny should be profoundly epigenetic and emergent, their order invisible from the genes!*¹⁹

As I pointed out in a previous paper:

An inevitable consequence of adopting the functionalist paradigm, and the notion that organic forms are ultimately contingent mechanical assemblages of matter [machines], is the need to postulate a genetic blueprint in the genes (analogous to the blueprint which specifies a machine) that specifies in detail the mature form. This is because contingent order, unlike natural form, cannot arise spontaneously as the result of natural law or from the self-organization of matter. If the types are indeed (as structuralists insist) natural forms like crystals, there is no need to specify in detail the higher order of the organic system in a detailed blueprint, because, as in the case of a crystal or any other natural form, “nature” takes the basic components (atoms, molecules, categories of biological matter) and organizes them into their native forms. Functionalism demands preformism (a detailed blueprint [in the DNA] specifying the final form), while structuralism implies epigenesis (emergent form based on self-organizational principles apart from any blueprint).²⁰

This is not the place for a systematic critique of the gene-centric, “bottom up” view of life, but as its demise is of central relevance to any defense of typology and of the “laws of form” biology, I think a short review is in order. For there is no doubt that if it had proved possible, as Lewis Wolpert and Julian H. Lewis claimed, “to compute [predict] the adult organism from the genetic information in the egg,”²¹ this would have gone a long way toward justifying the mechanistic, “preformist” paradigm and the notion that life’s basic forms are contingent assemblages as Darwinism implies. But the computations have never been carried out and the evidence for the mechanistic conception of form has remained stubbornly elusive.

a. The Demise of the Genetic Blueprint

The modern version of the genetic blueprint model was first formulated clearly by August Weismann,²² who was a convinced functionalist, mechanist,²³ and Darwinist. For him an organism was no more than a complex bundle of adaptations, and this complex of adaptations was a purely contingent mechanical arrangement of matter that, in his words, “could have been other than it is.”²⁴ The structuralist view, “that species are vital crystals,” he rejected.²⁵ Weismann envisaged the germ plasm to contain a set of genetic blueprints, analogous to the blueprints that specify the design of a machine. He called them “determinants,”²⁶ each of which specified a particular feature or trait of the adult phenotype in a highly deterministic, unidirectional way. Such a view would of course completely banish the notion of natural form from biology. As Marta Linde-Medina explains:

This [gene-centric] conceptualization of development makes the search for organizing principles a fruitless enterprise. If form is encoded in the genes, it is essentially arbitrary, and biological order is contingent. In this case, evolutionary biology becomes essentially a historical narrative and any regularity across taxa would be interpreted, not as evidence for the existence of natural laws—as it is the case in other sciences—but as historical contingencies now recorded in genes. The *arbitrariness of form* embodied in the idea of the genetic programme for development rules out the existence of an internal *cause* of biological

organization and thus represents the ultimate form of externalism in which natural selection is the organizing factor of organic form.²⁷

Precisely because the functionalist and Darwinian claim that life's order is artifactual logically necessitates gene-centrism, it is no coincidence that nearly all the founders of the mid-twentieth-century molecular biological revolution, including Jacques Monod,²⁸ Francis Crick,²⁹ and James Watson,³⁰ were strong gene-centric mechanists like Weismann, and fervently committed to the blueprint model. Given the logical necessity for blueprints to account for the transmission of *contingent* order through time, and given the adherence of modern biology to mechanism, it is little wonder the search for the blueprints in the genes, which would justify mechanism and the functionalist Darwinian paradigm, became the "holy grail" of twentieth-century biology.³¹

One of the most curious aspects of the whole century-long gene-centric saga, as I pointed out in a previous paper, is that, "despite the iconic status of the [genetic] blueprint model, there never has been at any stage in the history of genetics before and after 1953 any *clear* evidence that genes are any more than the building blocks of organisms... or *Aristotle's bricks*."³² As Frederik Nijhout comments: "Genes... act as suppliers of the material needs of development and, in some instances, as context-dependent catalysts of cellular changes... [but not] as 'controllers' of developmental progress and direction."³³ The preformist claim that the genome not only contains Aristotle's "bricks" but also a complete "plan of the house" has always been primarily a deduction from mechanism,³⁴ or at least has been powerfully influenced by the machine or organism metaphor,³⁵ which provides, as Evelyn Fox Keller pointed out in *Making Sense of Life*, "insulation from the ancient taint of animism."³⁶

That genes cannot be determinants of life's higher order is being increasingly confirmed by advances in knowledge of gene expression which are revealing that the meaning of genes is to a significant degree modulated by the cytoplasmic and cellular environment in which they are expressed:

The idea that genes are *unidirectional unambiguous determinants* of phenotypic traits is being massively undermined by the increasing evidence drawn from studies of eukaryotic gene expression... from stem cell research... from cloning... from studies of epigenetic imprinting and re[-]programming involving... DNA methylation and demethylation and post-translational modifications of histones and so forth... and from studies of RNA editing in human cells.³⁷

Increasingly, it seems that genes do not determine the phenotype of the cell "from below"; more and more, it looks as if the epigenetic physiological and biochemical state of the cell determines the meaning of the genes "from above." That the flow of genetic information is influenced to such a very large degree by environmental, cytoplasmic factors extraneous to the DNA means that Weismann's determinants can no longer be deemed the one-way directors of the "living symphony" that he initially envisaged, and as implied in the paraphrase of the central dogma "DNA makes RNA and RNA makes Proteins and Proteins make us."³⁸ To apply a linguistic analogy I used in a previous publication: "The English sound 'rite' may mean a variety of things from a direction to a legal term depending on the context in which it is uttered. Similarly the cytoplasmic

context in which the gene is expressed acts downwardly on the ‘gene’ to confer upon it biological meaning.”³⁹

Another development which undermines the classic, unidirectional, gene-centric model, a development of interest to cancer researchers and researchers in development, is the growing evidence that mechanical tensions in the cell membrane and in the architecture of cells (imposed by mechanical and biophysical stresses in the surrounding tissue in which the cell is stationed) can influence gene expression.⁴⁰ These studies imply that gene expression (in embryogenesis, for example) is highly interactive, with changes in tissue tensions and other global biomechanical and biophysical properties regulating gene expression.⁴¹ And this implies that regulation of gene expression in the embryo is profoundly influenced “top down” by the global state of the embryo.

Altogether, the growing evidence that gene meaning is context-dependent implies that *genes cannot be the sole unidirectional determinants of organic form, as Weismann and most geneticists throughout the twentieth century believed*. As I commented previously:

No wonder that there is among geneticists a widespread and growing perception that the classic blueprint model is outdated and insufficient... In a *Nature* opinion column commenting on the state of genomics, [Jim] Collins... is quoted as saying: “Although the Human Genome Project has expanded the parts list for cells, *there is no instruction manual* for putting them together to produce a living cell.” And in another *Nature* article on complexity... Mel Greaves confesses: “We fooled ourselves into thinking the genome was going to be a transparent blueprint, but it’s not.”⁴² [internal citations omitted]

b. Emergent, Self-Organized “Order for Free”

The major reason why there is, as Jim Collins complains, “no instruction manual”⁴³ in the genes specifying the higher order of life is that a considerable amount of higher order in biological systems is what is termed “emergent,” arising as a result complex self-organizing mechanisms. Such emergent order is invisible from below and by definition beyond genetic specification.

The topic of self-organization and emergence was never mentioned in *Evolution: A Theory in Crisis*, partly because of my own functional-ist stance at the time,⁴⁴ but also because self-organization was only just emerging as a serious possibility for building biological order.

Stuart Kauffman, in his impressive *Origins of Order*,⁴⁵ was one of the first scholars to advocate self-organization as an important source of biological order radically different from that specified in the genes, an emergent order which Kauffman famously described as “order for free.”⁴⁶ However, since the late 1980s many others have explored the conception, and the notion is now widely acknowledged to play a fundamentally important role in systems as diverse as the nest-building abilities of social insects, the folding of a protein, and embryonic development.⁴⁷ The unexpected emergence of self-organized complexity has been described as “magic” by Kauffman,⁴⁸ and by Scott Camazine et al. as defying “intuitive understanding [so that its] properties may seem to appear mysteriously.”⁴⁹ In short, all order generated by self-organization is what is termed

emergent, and is self-evidently epigenetic. The genes may specify the components of a self-organizing system, but the whole is generated out of the local interactions between the components.⁵⁰ This is “order for free” in the sense that it is order not specified by the genes. Of course, the self-organizing processes themselves are not “free” in a broader sense. They are dependent on higher-level natural laws that determine the properties of matter in the first place.

Two early advocates of self-organization as a means to generate emergent order were Alan Turing⁵¹ in the 1950s and Chomsky in the early 1960s. Chomsky, as discussed earlier (in Chapter 10) advocated self-organization as a way of accounting for the origin of human language several decades before the idea became mainstream. Another trailblazer for self-organization was Christian Anfinsen, who showed early in the 1960s that the folding of proteins comes about through self-organization, a discovery for which he was awarded the Nobel Prize.⁵²

c. Cellular Order

In at least one important field, cell biology, self-organization is now acknowledged to play a decisive role in the dynamic minute-to-minute reshaping of cytoplasmic organelles as well as the cytoskeleton and cyto-architecture.⁵³ As Tom Misteli explains:

Why does a cell not simply build stable, static structures? To change stable structures, dedicated machineries must exist to break them down and rebuild them again when needed. Self-organizing, dynamic structures can easily be modified by simple modifications of their subunits. The observed transitions of microtubular networks into spindles, and the complete, rapid disassembly and reassembly of... the Golgi complex, occur suddenly and typically with no significant intermediates. The absence of gradual intermediates in the reorganization of cellular structures is consistent with self-organization, as self-organizing systems are frequently in a state of criticality; that is, a point at which system properties can change suddenly.⁵⁴

In a remarkably prescient article, published some time ago in 1990, Franklin Harold reflected on the absence of what he called morphogenes specifying the shape of cells:

We know now many genes whose products are required for normal morphogenesis, and in a growing number the primary defect has been identified. However, successful completion of this demanding task brings one little closer to understanding either the normal shape or the mutant's aberrant one. There appear to be few true morphogenes (genes dedicated to specifying shape), at least in microorganisms... The great majority of morphologically abnormal microbial mutants represent defects in quite mundane metabolic or regulatory functions.⁵⁵

In a later paper Harold points out that because the cell's cytoarchitecture arises from the self-organization of the cell's constituents, the cell has no need for morphogenes:

The spatial organization of cells, including the arrangement of cytoplasmic constituents and the cells' global form, is not explicitly spelled out in the genome... Spatial order is not encoded anywhere at all but emerges from the interactions of the cell's molecular building blocks; it arises by *self-*

organization, like the specifications of a termite mound or the unique jumble of streets in my home town of Seattle. And the propagation of order down through the generations depends not on a codebook but on history repeating itself: the same building blocks, released into the same constraining context, will reproduce the same structures time and time again.⁵⁶

That cellular architecture arises from self-organization and not from detailed specification in the genes is obvious in the case of one of the simplest of all cells, the mammalian red blood cell (which was, as mentioned in Chapter 7, the subject of my postgraduate work at King's in London). In the case of the red cell, it is now well-established that its iconic biconcave shape arises as a result of the emergent biophysical and biomechanical properties of the cell membrane, that is, from the emergent physical properties of a complex collective of molecular membrane components, and not from any detailed specification in a genetic blueprint in the DNA. True, the genes specify the components of the membrane (Aristotle's bricks), but it is the emergent *non-specified* self-organized biomechanical properties of the molecular collective that makes up the membrane (Aristotle's house), generating the biconcave form of the cell. As the authors of a recent paper affirm, these mechanical properties are "encoded in the mechanical properties of the membrane,"⁵⁷ not in a genetic blueprint. That it is the emergent mechanical properties of the membrane that determine red cell shape has been confirmed by the recent success of modeling red cell form by utilizing directly measured emergent biophysical parameters or theoretically estimated parameters from knowledge of the hexagonal unit membrane structure.⁵⁸ Even some of the major deformation pathways, including those leading to the echinocyte and stomatocyte forms, have been captured in these models.⁵⁹ And what is true of the red cell form is also true of *all* other cells: Cellular order arises from the self-organizing properties of particular molecular collectives in the cell. The genes specify the bricks; self-organization builds the higher architecture.

Study of another cell, the mammalian photoreceptor, which has been the focus of my own research in human genetics over the past three decades, tells the same story. This cell is one of the most complex in the human body. Genetic defects in the cell cause retinal degenerative diseases like retinitis pigmentosa, and it has for this reason been the subject of very extensive genetic studies aimed at documenting all the genes responsible for these distressing retinal diseases.⁶⁰ Currently the genetics of the photoreceptor is perhaps more thoroughly documented, with the exception of the erythrocyte, than that of any metazoan body cell. Yet despite the thoroughness of the analysis there is no evidence that the complex architecture of these remarkable cells is specified in the genes. A recent paper I coauthored with two colleagues pointed out the lack of evidence that genes determine photoreceptor cell form and concluded:

Despite the intensity of the search for genes causing inherited retinal degenerations over the past 3 decades, of the approximately 200 disease genes identified to date, all appear to be ordinary housekeeping genes specifying proteins playing basic structural and functional roles in the mature photoreceptor cells. No genes or genetic elements have been identified which can be construed as having a specific morphogenic role, directing the development of the cytoarchitecture of any particular retinal cell. The evidence suggests that the cytoarchitecture of the retinal photoreceptors, although enormously complex,

arises from the self organization of the cells' constituents without any regulation or direction from an external genetic blueprint.⁶¹

At this time, one can assert definitively that to date no single cellular form has been computed, as Wolpert and Lewis envisaged,⁶² “from below.” And because it is now clear that so much of the cytoarchitecture of cells is emergent, it follows that no matter how exhaustively genes or gene circuits are studied in the future, it is never going to be possible to predict or see this emergent architecture from the genes—just as it is impossible to predict the unique physical and chemical properties of water from the properties of hydrogen and oxygen.

On a personal note, it was my own increasing recognition that the gene-centric paradigm was failing at the cellular level and that the architecture of cells is an “epigenetic affair,” the result of the self-organization of cellular matter, which was one of the major factors influencing my own move to structuralism.

d. Embryogenesis

Self-organization, and hence “order for free”—i.e., order not specified in the genes—also plays a critical role in embryonic development. Gastrulation, for example, is to a very large extent the result of emergent biophysical and biomechanical forces. As the authors of a recent paper point out:

Although it is rarely considered so in modern developmental biology, morphogenesis is fundamentally a biomechanical process, and this is especially true of one of the first major morphogenic transformations in development, gastrulation. Cells bring about changes in embryonic form by generating patterned forces and by differentiating the tissue mechanical properties that harness these forces in specific ways. Therefore, biomechanics lies at the core of connecting the genetic and molecular basis of cell activities to the macroscopic tissue deformations that shape the embryo.⁶³

Many authors have recently emphasized the important role that bio-mechanical forces play in shaping embryos. In another paper the authors comment:

Few would deny that physical mechanical processes are important in morphogenesis... Large scale movements of cells and tissues during embryo development involve force production leading to mechanical deformation. From this perspective a principle role of tissue stiffness and force production is to sculpt from the multicellular aggregate of the early embryo or to sculpt organs from germ-layers after the initial movements of gastrulation are complete.⁶⁴

The authors of another paper, pointedly entitled “Emergent Morphogenesis,” write of “[the capacity of] viscoelastic material properties of tissues to dictate the direction and speed of tissue movements as structures are sculpted.”⁶⁵ They also discuss the “mechanical integration of intracellular force generation with the local micro-mechanical environment to direct intracellular molecular-mechanical processes that manifest as a cell behavior” and “the mechanical integration of the cell, the micro-mechanical environment, and gene regulatory networks to direct cell differentiation.”

In another area, that of the development of the language organ in the human brain, we

have already seen that operational processing modules in the mature brain are not specified, as far as anyone can tell, by any blueprint in the genes, but must be assumed to be the result of self-organizational processes during brain ontogeny.

One of the most vigorous advocates of the notion that biomechanical and biophysical forces (acting beyond anything specified in the genes) sculpt embryos is Stuart Newman. As he shows in many recent papers, the physical properties of cells and tissues impose severe constraints on the way they spontaneously associate to form higher-order complexes and patterns. As he demonstrates, the biophysical properties of clusters of cells are capable of generating all manner of complex structures and patterns, including some of the major patterns of gastrulation.⁶⁶ In a recent interview he comments:

You can actually predict the kinds of physical forces clusters of cells [are] susceptible to and calculate that those physical forces are sufficient to cause some of the clusters to be hollow, multilayered, and segmented. Some of them will be elongated and some will have appendages.⁶⁷

In a recent paper, Newman and Ramray Bhat show how basic physical processes (again, none of which are specified directly by the genes) including cohesion, viscoelasticity, diffusion, spatiotemporal heterogeneity based on lateral inhibition, and multistable and oscillatory dynamics work together to “mold cell masses into only those morphologies which are characteristic of chemically and mechanically excitable mesoscopic materials, e.g., hollow, multilayered, elongated, segmented and branched forms.”⁶⁸ They continue: “But these are, in fact, the common morphological motifs of all metazoan body plans and organ forms, both in the invertebrates and vertebrates, appearing repeatedly over the course of evolution despite there frequently being no common ancestor between organisms with the same feature.”

In another recent paper Newman describes “three examples of morphological motifs of vertebrate bodies and organs, the somites, the skeletons of the paired limbs, and musculoskeletal novelties distinctive to birds, for which evolutionary origination and transformation can be understood on the basis of the physiological and *biophysical determinants* of their development.”⁶⁹ And in a comment that is supportive of the whole structuralist thrust of this book, he concludes:

I have argued that newer evidence from experimental embryology, interpreted in the light of concepts from condensed matter physics and physiology unknown at the time of Darwin and his early 20th century successors, challenges this tenet [Darwinism] and each of its components. This challenge does not outright abolish gradualist natural selection, but it does relegate it to a role in the fine-tuning and refining of heritable modifications that arise by other, often physiologically based, means.⁷⁰

Many other papers might be cited. Perhaps one additional very striking report is worth a mention, since it brings home with great force just how far embryonic sculpting is from the genes. The paper is again pointedly entitled: “The Role of Mechanical Forces in Dextral Rotation during Cardiac Looping in the Chick Embryo.”⁷¹ The subject is somewhat esoteric, but nonetheless the paper is indicative of the profoundly epigenetic direction in which biology is moving. From their study the authors conclude:

The results suggest that (1) the heart contains little or no intrinsic ability to rotate, as external forces exerted by the splanchnopleure (SPL) and the omphalomesenteric veins (OVs) drive rotation; (2) unbalanced forces in the [OVs] play a role in left–right looping directionality; and (3) in addition to ventral bending and rightward rotation, the heart tube also bends slightly toward the right... We feel that these results provide a better understanding of the biophysical mechanisms that regulate cardiac c-looping.⁷²

Richard Owen would have approved! Such *internal causal factors* are precisely what Owen and other pre-Darwinian biologists, and post-Darwinian biologists like William Bateson, were seeking in attempting to account for biological origins in terms of the natural properties of living systems.

In sum, an overwhelming body of evidence suggests that higher embryonic order, no less than the cytoarchitecture of cells, is largely emergent and arises from the self-organization of special categories of biomatter in the same way as protein, lipid, and microtubular forms (see below). A vast amount of organic order is clearly epigenetic and far beyond any sort of genetic reduction, and it will be the task of twenty-first-century biology to characterize and determine the basic nature of the self-organizational processes involved. But at present we can state definitely that between the genotype, the realm of genes, and the phenotype, the realm of emergent cellular and organismic form, there is in effect what amounts to a phase transition impenetrable from below. No matter how discomfiting it may be to the residue of gene-centrists and hard-line Darwinists, it is simply an uncontestable fact that the gene-centric reductionist agenda is in effect dead.

e. Protein Types as Self-Organizing Molecular Forms

One of the most remarkable of known cases where a set of biological forms arise by the self-organization of a particular category of matter (in this case, polypeptide chains) are the protein folds. On even the most cursory observation of the spatial deployment of atoms in a folded protein, one is struck by the staggering complexity of the arrangement. In fact, hardly any of the other novelties discussed above convey such an immediate impression of such very great complexity. Amazingly, the spatial organization of the several thousand atoms arises spontaneously as the result of self-organization.⁷³

As mentioned above, the discovery that the assembly of proteins was a matter of self-organization, unguided by any external input and perfectly replicable in a test tube, was one of the great discoveries in twentieth-century biology, for which Christian Anfinsen was awarded the Nobel Prize. Further, some of the physical rules that determine the few thousand possible protein folds have now been elucidated.⁷⁴ Remarkably, they amount to a set of “laws of form” remarkably reminiscent of the kind sought after by many nineteenth-century biologists.⁷⁵ These rules arise from higher-order packing constraints of alpha helices and beta sheets, which constrain possible protein forms to a small number of a few thousand structures.⁷⁶

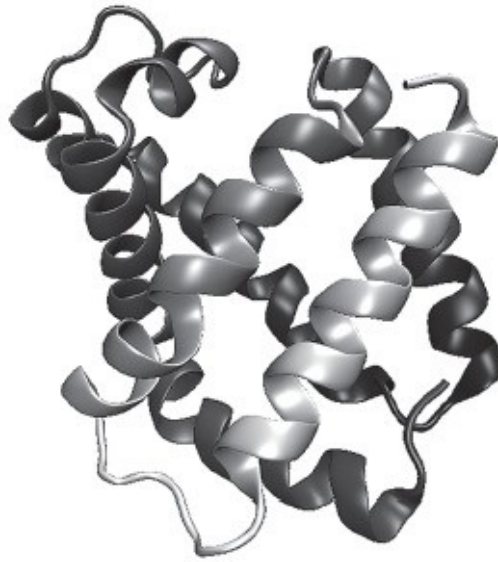


Figure 13-1. The Globin Fold. Belonging to the all-alpha-helix class of protein folds. The fold consists of eight alpha helices packed into a compact shape.

In conformity with pre-Darwinian structuralism one can consider the set of protein forms to be analogous to a set of crystals.⁷⁷ Moreover, all proteins exhibit adaptive modifications but these are, again, in perfect conformity with pre-Darwinian structuralism, clearly what Owen would have termed “adaptive masks,” built upon an underlying invariant non-adaptive form or “primal pattern.”⁷⁸ Thus the triosephosphate isomerase (TIM) barrel fold (an eight-stranded α/β barrel), has been adapted for more than sixty-one different enzymatic functions including TIM, enolase, and glycolate oxidase.⁷⁹ This implies that the same molecular architecture has been used again and again for very different adaptive ends.⁸⁰ Just as the pentadactyl “primal pattern” is adapted for flight, running, swimming, burrowing, etc., whereas the underlying form is essentially an abstract pattern which serves no *specific* adaptive end, so the TIM barrel is also basically an abstract “primal pattern” determined by the rules of protein folding, which again serves no *specific* adaptive end. Moreover, even the adaptations (adaptive masks) built upon the folds are almost certainly greatly constrained by the biophysical properties and the structures of the folds themselves. As Daniel Weinreich comments on one of his recent studies: “It now appears that intramolecular interactions render many mutational trajectories selectively inaccessible, which implies that replaying the protein tape of life might be surprisingly repetitive.”⁸¹

A folding polypeptide is drawn to its native conformation by a process of energy minimization. In effect the fold falls into what is very much a pre-existing energy pit or bowl, and the very terms used in the literature reflect this notion when they talk of “finding” or “filling” a pre-existing mold. Thus the folding process is often described as a mechanism by which “sequence selects structure.” As one author commented:

Thus, the notion that sequence determines structure might be more precisely formulated with the concept that sequence chooses between the limited number of secondary structure elements [determined *a priori* by the laws of nature or more specifically the protein folding rules, including the packing laws mentioned above] available to the polypeptide backbone.⁸²

As I mentioned in a previous paper:

In other words, it is not the sequence which specifies the mold but the mold which specifies which sequences can be accommodated. For the mold is prior to the sequence, although of course during folding each particular sequence is prior in time to the form which it finally makes manifest. The ubiquitous text book claim that “the amino acid sequence determines the 3D form of the protein” is a mechanistic interpretation of the folding process which might be more accurately stated Platonically as “the prior laws of form determine which amino acid sequences can fold into a stable 3D form.” If the sequence contains any information, it is not information to create or generate a unique artifact-like assemblage analogous to a Lego construct or a watch, but more of a guide through a pre-existing Platonic landscape to an already prefigured end.⁸³

My realization that the basic forms of the folds were immanent components of the world-order, determined by a set of “laws of form” and not by adaptation to serve particular functions, as the functionalist-Darwinian paradigm claims, was for me a personal “structuralist epiphany,” suddenly grasped one morning in the biochemistry department in Otago University in New Zealand (in corridor talk with colleagues, where all new insights are grasped in science!). I remember the moment quite clearly when I suddenly saw that all the homologs and *Bauplans* could similarly turn out to be immanent in nature and be determined by laws of form in the same sense as the folds. I immediately saw that it could be after all physics (as structuralists have always maintained) and not adaptation (as Darwin claimed) that has determined the basic forms of the organic realm.

f. Lipid Membranes as Self-Organizing Forms

The elucidation during the 1960s of the basic bilayer lipid membrane that forms the outer boundary of all living cells led to the discovery of another set of self-organizing structures which are clearly immanent in nature and determined by what are in effect another set of laws of biological form.⁸⁴ This is illustrated graphically by the fact that many lipid forms, strikingly analogous to those observed in the cell, can be generated *in vitro* in solutions of amphiphilic compounds by mere alteration of the concentration of the amphiphile, revealing that the forms are lawful structures determined by rules which constrain membrane forms to a limited set of basic structures. Philip Ball gives some dramatic examples of the way various lipid forms arise in different amphiphilic solutions.⁸⁵ As he points out, as the concentration of amphiphiles in an aqueous medium increases, eventually micelles form; and as more surfactant is added, plane lamellae form; and as the concentration of the lipid is increased even more, a bicontinuous phase is formed consisting of a vast labyrinth of interconnected tubes.

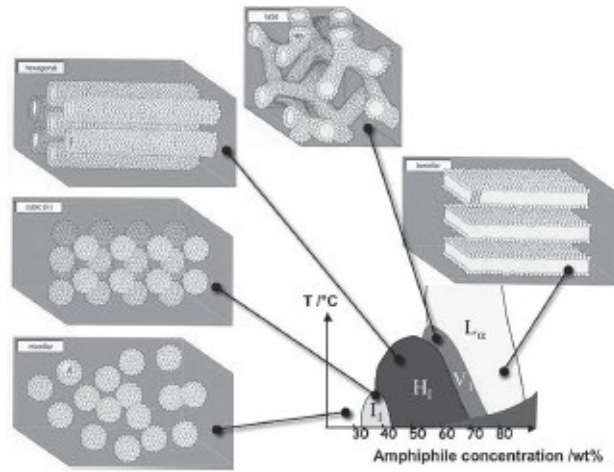


Figure 13-2. Self-organized Lipid Forms. They are generated by simply increasing the amphiphile concentration in an aqueous solution.

Overall, this evidence suggests that many of the core lipid forms that play a vital role in the generation of cellular and subcellular order are—like the protein folds—intrinsic natural forms. Again, we can conceive of them as being drawn into pre-existing energy minima. In living systems these basic lipid forms (primal patterns), like the protein folds, are modified to serve specific adaptive ends (adaptive masks) by changes in the chemical composition of the membrane.⁸⁶ The same basic membrane structure (the primal pattern) is utilized to form the endoplasmic reticulum, to enclose the nucleus and the mitochondria, to form the chloroplast, and to form a vast variety of tubes, vesicles and sheets. Waddington commented on these modifications:

The tube... [may be considered] a vesicle in which one dimension is very much elongated... the majority of subcellular organelles are built up as complexes of vesicles, diderms (two-skinned vesicles), and tubes... Golgi bodies, for instance, consist essentially of a pile of flattened vesicles... Mitochondria again are complex closed vesicles constructed out of two membranes.⁸⁷

Although, like the protein folds, each specific lipid form—like the lamellae of the chloroplast or the outer segment of the photoreceptor—is adapted to serve some particular function (photosynthesis in the case of the chloroplast; phototransduction in the case of the photoreceptor outer segments), and each represents an “adaptive mask,” there is no doubt that the underlying form—layered stacks of bilayer lipid membranes—is primarily determined purely by physical law and indeed can be considered, like the folds, to be immanent in nature.

g. Self-Organizing Microtubular Forms

The microtubular aster is another example of a complex molecular form that arises by self-organization. The aster is generated by the spontaneous interactions between microtubules and molecular motors, arising from “the intrinsic characteristics of its parts.”⁸⁸ As described by Marc Kirschner and Tim Mitchison, during its formation, the developing spindle appears to be searching for a pre-ordained natural energy minimum, which it eventually “finds” via a seeming “infinity” of different routes, and not via a unique, precisely specified mechanical assembly pathway, as occurs in the case of phage.⁸⁹

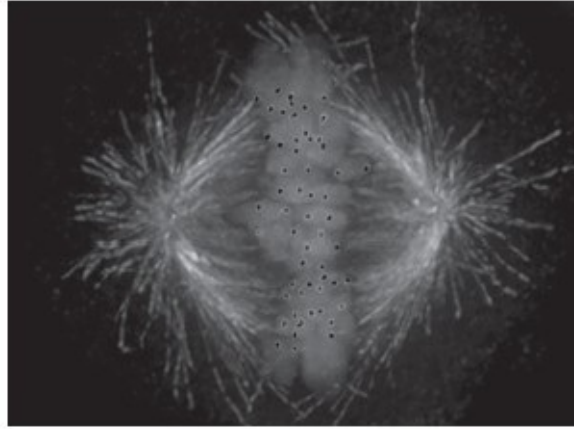


Figure 13-3. The Spindle Apparatus.

The aster is only one of several well-defined, self-organized, microtubular forms, several of which may be generated *in vitro* in a Petri dish⁹⁰ or simulated *in silico*⁹¹ merely by changing the basic constituents in somewhat analogous fashion to the lipid forms mentioned by Ball (see above). And microtubular forms are not unique. As Karsenti points out, actin and myosin molecules can also self-organize in a Petri dish into a variety of forms, including ring structures.⁹²

So by modification of the molecular environment in which microtubules self-organize, a vast variety of complex structures can be generated, including the very complex, adaptive, microtubular structures which play such a crucial role in the determining the forms and functions of cells.⁹³ Moreover, during the self-organization of the aster, the basic elements can be thought of as being drawn toward an energy minimum,⁹⁴ a “strange attractor” analogous to those involved in protein folding.

In all of the above three cases, the final biological form is not specified in the genes. The genes specify the building blocks, but these then self-organize into the higher-order forms, which are epigenetic and emergent.

13.3 Robustness and Developmental Systems Drift

The fact that regenerated organs are, as Amundson pointed out, “clearly homologous to those originally developed in embryos, but ... constructed in a different manner and often from different tissue sources”⁹⁵ has always been seen as evidence that organic forms possess a special robustness. Hans Driesch cited many examples in his *Science and Philosophy of the Organism*, and saw the phenomenon as indicative of a vital force, which he called the *entelechy*.⁹⁶ Some examples are indeed so remarkable that Driesch can be forgiven for claiming them as evidence for his vitalism. In the case of the newt, for example, many organs in the body can be regenerated after surgical excision from the adult organism—including limbs, tail, and the lens and retina.⁹⁷

Another type of robustness that is also supportive of the notion that the homologs are emergent, self-organizing, natural forms is the phenomenon termed “developmental systems drift,”⁹⁸ *witnessed when the same homologous structure arises in different ways in different species and involves different genes and genetic pathways*.⁹⁹ To cite a classic example, the early embryos of all vertebrates—e.g. reptiles, amphibians, birds, and mammals—are very similar at the post-gastrula stage (the phylotypic stage), when the vertebrate body plan is first apparent, but the developmental processes and pathways that

lead to this homologous stage differ markedly in different classes. Another example, discussed above, is the diversity of cytological routes to an identical angiosperm gametophyte. These same advances in developmental genetics have revealed that the homologies are even more robust than previously believed. Despite the utilization of some of the same basic elements of the toolkit (Hox proteins, etc.) in the case of many homologs, there is massive underlying genetic and developmental variance in the way the toolkit is employed in different species to achieve the same homolog or end,¹⁰⁰ an observation highly consistent with (even if it does not prove) the view that homologs are indeed immanent in nature and not artifacts of time and chance.

In a recent paper, I considered developmental systems drift in the context of insect segmentation:

One might have imagined that the underlying developmental genetic mechanisms that so stringently conserve the [insect] body plan would have been themselves stringently conserved—an assumption which would lend itself to a gene-centric/functionalist account. But in fact, three different mechanisms are utilized to generate segments, even among closely related species within one insect order (among beetles, for example). Although the segmentation pattern of all adult insects is the same—three thoracic segments, and no more than eleven abdominal segments—three different developmental mechanisms are used to generate segments in different species, the so called short germ-band, intermediate germ-band, and long germ-band. In long germ-band development, the entire anterior-posterior segmentation pattern is determined simultaneously in the embryo, while in short germ-band development the segments are generated by successive temporal subdivision of a posterior growth region. In the first case, a spatial sequence is formed *all at once*, whereas in the other a spatial sequence is *also a temporal sequence*.¹⁰¹

Paul Liu and Thomas Kaufman also comment on the same phenomenon:

The insect body consists of a head of six or seven segments, a thorax of three, and an abdomen of eight to 11 segments, and is essentially invariant across species. Although it makes intuitive sense that differing developmental mechanisms should lead to differing final morphologies, the converse seems counter-intuitive; that differing developmental trajectories should arrive at the same endpoint. Yet this is the case with insect segmentation.¹⁰²

Curiously, the same radical switch between simultaneous specification and temporal specification also occurs in the case of the pentadactyl limb. While in most species the digital pattern emerges simultaneously (like short germ-band segmentation in *Drosophila*), in certain species the digits are formed sequentially in a temporal succession from digit one to digit five.¹⁰³ So again the same “higher” pattern is derived in two radically different ways. Many other cases of extremely different generative means to the same homolog might be mentioned, including polyembryos in parasitic wasps, where an individual fertilized egg divides multiple times, giving rise to a mass of undifferentiated cells (a polygerm) which then splits into clusters of cells, each cluster forming an embryo which develops into a “normal wasp”—again a radical departure from the canonical embryogenesis followed in most wasp species.¹⁰⁴ And of course, as we have seen, the same

phenomenon of radically different routes to the same end occurs in angiosperm gametophyte development.

Another case of conservation of form in the face of radical changes in lower-level gene circuits and developmental mechanisms is witnessed in the generation of the chordate body plan in vertebrates and their closest invertebrate chordate cousins, the tunicates. As Tanguy Chouard comments in a *Nature* article:

Tunicates—also known as sea squirts—are humans’ closest invertebrate cousins. They have tadpole-like larvae that closely resemble miniature vertebrate embryos and so were expected to build their bodies in the same way. But they don’t. Most of the “organizer genes” are there in the tunicate genome, but they are expressed elsewhere in the embryo and do dramatically different things. It’s as if you had found a car in which components of the engine were scattered all over the back seat—but the car still worked.¹⁰⁵

These extraordinary revelations of the stability of homologs or novelties in the face of different generative processes in different species constitute only a tiny fraction of the growing inventory of cases that support the notion that the homologs are indeed robust, emergent, natural kinds. Günter Wagner, whose research agenda is focused on the ontological status of the homologs, comments:

Developmental mechanisms and pathways have a tendency to shift under the continuing presence of the “developmental” type. For instance, the genetic machinery that produces segments in grasshoppers is in important ways different from that in a fruit fly. Genes which are essential for fruit fly segmentation are not even expressed during segmentation in grasshoppers, e.g., even skipped and ftz.¹⁰⁶

Wagner concludes: “There is *no explanation for the phylogenetic stability of developmental types*... This is, according to Amundson, and I follow him in his argumentation, the most urgent theoretical problem in the re-unification of development and evolution.”¹⁰⁷

So here is a deep enigma. The homologs are “generated” in different ways involving different genes, different gene circuits, etc., and at the same time they are adapted in many diverse ways to serve different adaptive purposes. They persist unchanged in the face of generative changes “below” and adaptive changes “above.” What explanation can be offered for this primal observation other than that the homologs are some type of natural form? Surely they are more like natural forms than the “contingent assemblages of matter” that Darwinism implies?

Acting like “strange attractors,” these robust, enigmatic, primal patterns have exerted a mysterious determinate influence on the biomatter in which they act and have done so faithfully, in diverse lineages, in diverse ways, over hundreds of millions of years, over periods of cosmic time beyond ordinary human comprehension, shaping by their mysterious powers the overall hierarchic pattern of life on earth.

13.4 The Forms of Water

Despite the mounting evidence that at least some of the higher architecture of life arises

from the self-organizing properties of matter, and despite the fantastic complexity of material forms so ubiquitous in the inorganic realm, a critical reader may still have doubts. How could natural laws or the emergent properties of various categories of biological matter shape complex biological structures such as the novel homologs that have been the focus of this book?

To see how this claim is far from implausible, consider the various forms that one of the simplest of all substances, water, adopts under the agency of natural law.



Figure 13-4. A Splash of Water.

The succession of different material forms which arise in a purely homogeneous body of water as its mass increases is very suggestive. One molecule of water is insufficient to make a round drop of water. But billions will form a small drop, which will adopt a spherical shape fashioned by surface tension. As the mass of the drop increases, it adopts a pear shape given by surface tension and the force of gravity on earth. As the amount of water in the drop increases, eventually gravity pulls it to the ground, and if it falls into a pool of water, it makes a characteristic splash, a complex form which exists only for an instant, consisting of a thin circular wall of liquid surmounted by a circle of small drops (see Figure [13-4](#)). This form eventually falls back into the liquid, causing a series of small waves to radiate out from the point at which the drop hits the water.

In this example, a whole succession of forms is generated by different natural laws and different physical processes that apply to different masses of the same substance, water. Note also that the change is not always continuous. The moment when the drop falls to the ground is a strikingly saltational event, while the growth of the drop before it falls is a very gradual process. In the case of a developing embryo, the situation is far more complex, because the matter of the embryo is not only massively heterogeneous compared with water, but changing continually as patterns of gene expression change during development. The lesson: If water under the agency of natural law can be shaped into such diverse natural forms, it is hard to refuse the possibility that complex, unexpected, emergent form, from the molecular to the organismic level, may also arise under the agency of natural law in biological systems.

13.5 Thesis and Antithesis

I have referred to typology as the “default position,” arguing that if Darwinism fails, i.e., if the actualization of the novel homologs during the history of life cannot be accounted for in terms of cumulative selection during phylogeny and gene-centrism during ontogeny,

then the plausibility of the nineteenth-century “laws of form” biology and the notion of the homologs as atom-like natural forms is greatly enhanced.

Indeed, in many ways, the typological worldview is the logical antithesis of its Darwinian successor. Where typology saw the Types to be real natural elements (forms) of the world-order (analogous to atoms and crystals) generated by “laws of form,” Darwinism implied that they were contingent assemblages generated by natural selection, accidental products of time and chance, and the *Bauplans* mere residues in extant organisms.¹⁰⁸ For typologists, life’s basic order (the Types) is lawful; for Darwinists, all or the vast majority of biological order is contingent. Whereas for Darwinism adaptation is primary (indeed, it is all that there is), for typology it is secondary, grafted onto the underlying non-adaptive primal patterns or homologs. Where Darwinism sought to account for the order of living things within an externalist adaptive framework, typologists like Owen sought internalist, formalist explanations for life’s underlying primal order: Owen’s polarizing force,¹⁰⁹ or H. G. Bronn’s natural creative force.¹¹⁰ If typology is right, then life on earth must be assumed to be an integral part of the world-order, its forms no less “intended” than the forms of the inorganic world, and life on earth the outcome of a generative program analogous to that which generates the atoms of the periodic table in the stars.

In an intriguing comparison of the views of Owen and Darwin in his preface to *Richard Owen: Biology without Darwin*, Rupke captures the opposing components of their respective worldviews and the great dichotomy between structuralist and functionalist thinking:

Owen represented “biology without Darwin” in more than one sense. The two great naturalists differed above all about the nature of organic evolution. They held opposing views on the origin of life from lifeless matter (Owen postulated multiple spontaneous “emergences”; Darwin kept the issue at arm’s length), on the mechanism of species development (Owen stressed an inner, “genetic” cause, Darwin external, natural selection), on the pattern of evolution through geologic time (Owen saw in it a structural logic, Darwin the haphazardness of contingency), and on “man’s place in nature” (Owen stressed the unity of humanity and its distance from the apes; the Darwinians constructed close racialist links between “lower humans” and “higher apes”). In addition, Owen tried, much more than Darwin, to bring processes of morphogenesis to bear on the origin of species, and as such he was an early representative of what today we refer to as evo-devo, the field of evolutionary biology that integrates the study of how individual organisms develop with the development of species.¹¹¹

13.6 Summary

In this chapter, I have presented three lines of evidence which support the structuralist and typological view that the basic forms of life on earth are part of the order of nature and that the novelties which define the Types are robust natural forms: (1) the discovery of the cosmic and chemical fine-tuning of the laws of nature for life as it exists on earth; (2) evidence that much of the order of life is self-organized and epigenetic, generated by emergent biophysical and biomechanical forces which are beyond computation from the genes; and (3) the extraordinary robustness of the homologs.

Admittedly the evidence at present does not allow us to conclude that any of the specific taxa-defining homologs—hair, pentadactyl limb, diaphragm, feathers, particular *Bauplans*, etc.—are indeed like atoms and crystals, ultimately arising from the properties of matter.¹¹² It may in fact be many decades before the ontological status of the homologs is finally established. Nonetheless, the move now well underway to a twenty-first-century epigenetic biology, while it does not prove Owen right or validate in any final sense the structuralist framework, is the first and necessary move that must be taken if a new typology is eventually to emerge. And when these three lines of evidence are taken together, in conjunction with the failure of Darwinism to account for the origin of the homologs, I think the consilience is highly suggestive.

14. The Priority of the Paradigm

It seems clear to me that the species is not a life-crystal in the sense that it must, like a rock-crystal, take the form in a particular way and in no other for purely internal reasons and by virtue of its physical constitution; the species is essentially a complex... of modern adaptations which have been recently acquired, and of inherited adaptations handed down from long ago—a complex which might quite well have been other than it is... if it had originated under the influence of other conditions of life.

August Weismann, *The Evolution Theory* (1904), Volume Two, 307.

Despite its obvious failure, Darwinism has retained its hypnotic hold on the biological mind primarily because cumulative selection has been “the only game in town.” As Thomas Kuhn pointed out, without an alternative framework, scientific communities are forced to regard evidence that to anyone outside the circle of belief may appear to be profoundly hostile as mere anomalies.¹

The perception that Darwinism is “the only game in town” has been reinforced since the middle of the twentieth century by makers of the neo-Darwinian “modern synthesis,” who imposed on biology the conviction that the evolutionary argument was over, and that the Darwinian functionalist paradigm had won the day. In their view, adaptation was everything—the primal organizing principle of biology—and the extrapolation from microevolution to macroevolution was embedded in concrete.²

Not content with conjuring up a completely illusory Darwinian victory, the makers of the neo-Darwinian synthesis also denigrated nineteenth-century typologists and structuralists, portraying them, as we have seen, as intellectually driven by discredited metaphysical, essentialist beliefs which biased their biology in favour of the notion of the Type. This denigration of typology was a striking case of the “pot calling the kettle black.”

The apparent lack of a rational scientific alternative has meant that the defects and failures of Darwinian metascience are viewed by nearly all evolutionary biologists as trivialities which will somehow eventually be accounted for in terms of the accepted theory. For this reason, virtually all current evolutionary biologists, *even those who are insistent that Darwinism is insufficient*, are stalled at an intellectual Rubicon, unable to cross—intuiting that Darwinism cannot provide a convincing narrative, yet having no alternative view of nature to embrace.

Most of the novel evolutionary mechanisms currently on offer to account for the origin of evolutionary novelties, including phenotypic plasticity, epigenetic innovation, facilitated variation, multilevel selection, and so forth, are essentially conservative amendments to the current paradigm.³ Such amendments do not provide anything like an alternative *causal directing agency* to replace cumulative selection as a means of building “infinite complexity,” of crossing the great divides and accounting for the origin of the homologs. None of them can provide a plausible account of the origin of such homologs as the feather, human language, hair, the angiosperm flower, the insect body plan, and so forth.

And if cumulative selection fails, then what *natural* explanation, what directive natural force, is available other than natural law? What explanation other than the fitness-structuralist paradigm, which sees the forms of life as no less built into nature than the properties of water? If the homologs are not natural forms—not part of the “furniture”⁴ of the universe as Wagner refers to them—given their uniqueness, their complexity, their apparently saltational emergence during phylogeny and subsequent invariant constraining powers for vast periods of time in diverse lineages, then to what other category of being do they belong?

Fortunately, it now seems that after a slumber of more than 150 years, a consilience of evidence is emerging that is supportive of the alternative paradigm of natural law. There is the deep hint—arising from the cosmological discovery of the fitness of nature for life—that the life forms on earth may be, after all, *an integral part of the cosmic order*. There are tantalizing hints that an explanation of life’s origin may lie within the fitness-structuralist framework, i.e. hints that nature lent a hand over this first great divide! There is increasing evidence—perfectly consonant with the structuralist view—that a great deal of organic order is emergent, the result of the self-organization of different categories of biomatter and not specified in the genes as the alternative Darwinian contingent model predicts. There is the evidence of evo-devo that the paths of evolution have been constrained by deep homologies, shared in some cases by all metazoan organisms, and that the specific taxa-defining novelties themselves have been shaped largely by internal causal factors rather than cumulative selection. Finally, there is the existential challenge to Darwinian functionalism posed by the non-adaptive nature of so many of the homologs and *Bauplans*.

In the context of this consilience, the various failures of Darwinian externalism can no longer be viewed as anomalies but rather as straws in a potentially revolutionary wind, heralding a coming shift to a more structuralist, internalist, twenty-first-century biology. At last, there is *another* game in town. No longer can Owen’s perception, and that of many pre-Darwinian biologists, of the Types as natural forms generated by special laws of biological form be dismissed simply as metaphysical nonsense.⁵

But sadly, because of an unshakeable commitment to the contingent view of life—and perhaps because to embrace a biology of law might be seen as the first step towards a reintroduction of teleology into biology—many Darwin skeptics among evolutionary scientists are unable to cross the dangerous waters and leave behind the realm of contingency.

This is obvious on any reading of Fodor and Piattelli-Palmarini’s *What Darwin Got Wrong*. The authors argue fervently—along with many others—that Darwinism cannot be the answer. But they end their book with a whimper with these massively disappointing words: “‘OK; if Darwin got it wrong, what do you guys think is the mechanism of evolution?’ Short answer: we don’t know what the mechanism of evolution is.”⁶

There is no doubt that, as Fodor and his co-author insist, Darwin got it wrong. But although the Darwinian dragon is fatally wounded, to account for the “third infinity” and the novel homologs without the slightest hint of teleology, the beast must be maintained on life support by evolutionary biologists. This is why Pigliucci and Kaplan end their critical book *Making Sense of Evolution* with the claim, diametrically opposed to that of

Fodor and Piattelli-Palmarini, that Darwin “was (largely) right after all.”⁷ Indeed, Darwinism will have to be right after all, will always be resuscitated, will *have to be* resuscitated, even in the face of Bateson’s “endless absurdities” and Owen’s non-adaptive *Bauplans*, even when it is so obvious that “he got it *wrong*,” until evolutionary biologists put aside their metaphysical commitment to a contingent worldview, and biology finally embraces the realm of law—a realm whose only defect in the eyes of the agnostic mainstream is that it *might be construed* as supporting a return to a more teleological view of life and its place in the cosmos.

Darwin is dead; yet—like the ancient King of the Woods who stood sentinel over the Golden Bough in Diana’s sacred grove at Nemi—Darwin relives! *Le roi est mort, vive le roi.*⁸

I have shown here that the core thesis of *Evolution: A Theory in Crisis* has been vindicated by advances over the past three decades. Nature remains as I described her in 1985: stubbornly discontinuous, resistant to all attempts to reduce her to Darwinian functional continuums. From the origin of life to the origin of human language, the great divisions in the natural order are still as profound as ever, and still uncrossed either by known empirical series of adaptive transitional forms or by hypothetical functional continuums. Darwin was *not* “right after all.” There is an irresistible consilience of evidence for rejecting Darwinian cumulative selection as the major driving force of evolution. And what makes this consilience of evidence against Darwin so significant is that it is precisely what we should expect to see if—as many biologists before Darwin believed—the Types are real existents in the order of nature.

Evolution is still a theory in very deep crisis. And as the arguments and much of the evidence I have presented here suggest, the only resolution to the ongoing crisis is the adoption of a new, twenty-first-century version of “laws of form” biology in which the basic “Types” would no longer be seen as artifactual assemblages, as they have been since 1859, but as lawful natural forms comparable to the forms of the inorganic realm.

Only by rejecting the “contingent narrative” can biology be restored to its rightful place in the lawful and rational realm of natural science. Only by rejecting the “contingent narrative” can the inorganic and organic realms be united in the same causal framework.

As alluded to above, I do concede that such a “lawful biology” might be seen as a first step back to teleology and the notion that the laws of nature are “intelligently” fine-tuned to generate the set of life forms on earth up to and including mankind. Indeed, although the Types and “primal patterns” are embedded in matter, they may be construed as many pre-Darwinian biologists did: as reflecting a reality beyond matter, *a la* Platonic forms.

However, my claim that life is an integral part of nature is not an argument for design or a defense of Plato’s cosmology, but an ontological verdict on the fabric of reality, on the ground of being. Whether or not the fitness of that fabric for life on earth is ultimately the result of design has no bearing on whether life is an integral part of nature or whether the universe is in some sense biocentric. Whatever the ultimate cause of things, whatever teleological implications or otherwise may be inferred, the validity of structuralist claims and my advocacy of a lawful biology are supported by *the scientific evidence*.

Although I am convinced that the structuralist view is increasingly supported by many lines of evidence, I am aware that all scientific hypotheses are in the end provisional. It is perfectly possible that the phenomenon of life may ultimately prove to be beyond any explanation in terms of either the structuralist or functionalist frameworks. The causal answer may lie in models of nature as far removed from present-day conceptions as quantum physics is from Newton's *Principia*. Given that the sheer complexity of living systems is already beyond ordinary comprehension, in the last analysis nature may be, as J. B. S. Haldane famously proclaimed, "not only queerer than we suppose, but queerer than we *can* suppose"—and certainly far, far queerer than conventional Darwinism supposes.⁹

Endnotes

Chapter 1—Introduction

1. Michael Denton, *Evolution: A Theory in Crisis* (Chevy Chase, MD: Adler & Adler Publishers, 1986), 353.
2. *Ibid.*, Chapter 5.
3. Denton, *Evolution: A Theory in Crisis*, Chapter 5; Ernst Mayr writes: “A triangle illustrates essentialism: all triangles have the same fundamental characteristics and are sharply delimited against quadrangles or any other geometric figures. An intermediate between a triangle and a quadrangle is inconceivable.” [“Darwin’s Influence on Modern Thought,” *Scientific American* (July 2000): 81–82.]
4. D’Arcy W. Thompson, *On Growth and Form*, 2nd ed. (New York: The Macmillan Company, 1945), 1094, available online at <https://archive.org/details/ongrowthform00thom>.
5. Denton, *Evolution: A Theory in Crisis*, 90–91, 213, Chapter 5; also see Frietson Galis and Johan A. J. Metz, “Evolutionary Novelties: The Making and Breaking of Pleiotropic Constraints,” *Integrative and Comparative Biology* 47, no. 3 (September 2007): 409–419, doi:10.1093/icb/icm081. I still believe that a convincing argument against any sort of major evolutionary change can be mounted, based on the intense functional integration of living things.
6. Denton, *Evolution: A Theory in Crisis*, 90–91, 213, and Chapter 5; also see Galis and Metz, “Evolutionary Novelties: The Making and Breaking of Pleiotropic Constraints.”
7. For a modern edition of Owen, see Richard Owen, *On the Nature of Limbs: A Discourse*, edited by Ronald Amundson (Chicago: University of Chicago Press, 2007).
8. Günter P. Wagner, *Homology, Genes, and Evolutionary Innovation* (Princeton: Princeton University Press, 2014).
9. Colin Patterson, “Morphological Characters and Homology,” in *Problems of Phylogenetic Reconstruction*, edited by Kenneth Alan Joysey and Adrian E. Friday (New York: Academic Press, 1982), 21–74; Patterson defined homology as synapomorphy, 29 (see reference to Patterson in Wagner, *Homology Genes and Evolutionary Innovation*, 74–75); a synapomorphy is a homolog shared by two or more taxonomic groups inherited from a common ancestor (the pentadactyl limb in various tetrapod groups); an apomorphy is a homolog shared by the members of a particular group but not present in an ancestral form (hair in mammals); Ian J. Kitching, Peter L. Forey, Christopher J. Humphries, and David M. Williams, *Cladistics: The Theory and Practice of Parsimony Analysis*, 2nd ed., The Systematics Association Publication No. II (New York: Oxford University Press, 1998), Chapter 1, 2–3.
10. Richard Owen, *On the Nature of Limbs* (London: John Van Voorst, 1849), <https://archive.org/details/Owen1849br46D>.
11. Stephen Jay Gould, *The Structure of Evolutionary Theory* [henceforth *SET*] (Cambridge, MA: Belknap Press [Harvard], 2002), Chapters Four and Five; Ronald Amundson, *The Changing Role of the Embryo in Evolutionary Thought*, Chapter 3.
12. Gould, *SET*, 252.
13. *Ibid.*, Chapter 4.
14. Richard Owen, *On the Anatomy of Vertebrates*, vol. 3 (London: Longmans, Green and Co., 1866), 809.
15. Edward Stuart Russell, *Form and Function* (London: Murray, 1916), 241; Gould, *SET*, 1070–1071.
16. Michael J. Denton, “The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism,” *BIO-Complexity* 2013, no. 3 (2013): 5, doi:10.5048/BIO-C.2013.3.
17. Owen, *On the Nature of Limbs*.

18. Wagner, *Homology, Genes, and Evolutionary Innovation*, 20.
19. Denton, "The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism," 1.
20. Nicolaas Adrianus Rupke, *Richard Owen: Biology without Darwin* (Chicago: Chicago University Press, 2009), Chapter 4, 113.
21. Denton, "The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism," 5.
22. Denton, *Nature's Destiny: How the Laws of Biology Reveal Purpose in the Universe* (New York: Free Press, 1998), and Denton, "The Place of Life and Man in Nature: Defending the Anthropocentric Thesis," *BIO-Complexity* 2013, no. 1 (2013): 1–18, doi: 10.5048/ BIO-C.2013.1.c.
23. That Darwin himself saw organisms to be nothing more than complex functional mechanical assemblages—bundles of adaptations built up bit by bit to satisfy a series of historical environmental challenges—is clear in this well-known passage: "If a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct forms." [Charles Darwin, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects*, 2nd ed. (London: John Murray, 1882), 238–239.] That modern-day hard-core Darwinists have stuck to the machine analogy is obvious on any reading of George Williams, Jacques Monod, Richard Dawkins, or Daniel Dennett.
24. Russell, *Form and Function*, 78.
25. John Ray took the pan-adaptational stance to extraordinary lengths in his *The Wisdom of God Manifest in the Works of Creation*, where he writes: "The Body of Man may thence be proved to be the Effect of Wisdom because there is nothing in it deficient, nothing, superfluous, nothing but hath its End and Use;" page 228 "Nature hath not given Paps to Men, either to no Purpose, or for meer [sic] Ornament, but, if Need requires, to supply the Defect of the Female, and give Suck to the Young." John Ray, *The Wisdom of God Manifest in the Works of Creation*, 7th ed. (1717) digitized by John McKeown, John Ray Initiative, http://www.jri.org.uk/ray/wisdom/wisdom_of_god.pdf, 227.
26. Gould, *SET*, Chapters Four and Five.
27. The notion implicit in the functionalist view of life which came to dominate biology after Darwin, that organisms are ultimately artifactual beings analogous to machines (i.e., no more than complex functional or adaptive assemblages of parts), long predated the Darwinian revolution. In the seventeenth century, Descartes claimed in his *Treatise on Man* that the human body was a complex machine whose functions: "follow naturally ... entirely from the dispositions of the organs—no more nor less than do the movements of a clock or other automaton, from the arrangement of its counterweights and wheels" [René Descartes, *Treatise on Man* (New York: Prometheus Books, 2003), 113]. See also his *Discourse on Method* and *Principles of Philosophy*. English natural theology also adopted the mechanistic analogy, as witnessed by Ray's *The Wisdom of God as Manifest in the Works of Creation* and Paley's *Evidences*.
28. Gould, *SET*, Chapter 7; Amundson, *The Changing Role of the Embryo in Evolutionary Thought*.
29. Massimo Pigliucci and Gerd Müller, eds., *Evolution, the Extended Synthesis* (Cambridge, MA: MIT Press, 2010). See Chapter 1 by Pigliucci and Müller, "Elements of an Extended Synthesis," and Chapter 17 by Werner Callebaut, "The Dis/Unity in the Evolutionary Synthesis and its Extensions"; See also Gould, *SET*, Chapter 7.
30. Amundson, *The Changing Role of the Embryo*.
31. Thompson, *On Growth and Form*.
32. Lev Berg, *Nomogenesis: Evolution Determined by Law* (Cambridge, MA: MIT Press, 1966), 149.
33. Hans Driesch, *The Science and Philosophy of the Organism* (London: A. C. Black, 1929).
34. Arthur Koestler, *The Case of the Midwife Toad* (New York: Vintage Books, 1973).

35. In *The Origin of Species* (1972), Chapter 5, 108–111, Darwin discusses the effects of use and disuse of parts and considers the possibility of mutilations being inherited. In Chapter Fifteen, Darwin talks about natural selection being aided by the use and disuse of parts, 416, 426, 429 (the last page of the book!).
36. Gould, *SET*, 576–579.
37. *Ibid.*, 576.
38. Quoted in Gould, *SET*, 577 from William White Howells, *Mankind in the Making: The Story of Human Evolution* (Garden City, NJ: Doubleday, 1959), 24.
39. *Ibid.*, 577.
40. Stephen Jay Gould and Richard Lewontin, “The Spandrels of San Marco and the Panglossian Paradigm: A Critique of The Adaptationist Programme,” *Proceedings of the Royal Society of London, Series B* 205, no. 1161 (1979): 581–598.
41. Gould used the term in his introduction to Björn Kurtén, *Dance of the Tiger: A Novel of the Ice Age* (New York: Random House, 1980), xvii–xviii.
42. Jerry Fodor and Massimo Piattelli-Palmarini, *What Darwin Got Wrong* (London: Profile Books Ltd., 2010).
43. Stephen Jay Gould, “Evolution’s Erratic Pace,” *Natural History* 86, no. 5 (1977): 12–16; <http://creation.com/that-quote-about-the-missing-transitional-fossils>; Stephen Jay Gould, *The Panda’s Thumb: More Reflections in Natural History* (New York: Norton, 1992).
44. Colin Patterson, *Evolution* (London: The British Museum of Natural History, 1978); Brian G. Gardiner, Philippe Janvier, Colin Patterson, Peter L. Forey, Peter Humphrey Greenwood, Roger S. Miles, and Richard P. S. Jefferies, “The Salmon, the Lungfish and the Cow: A Reply,” *Nature* 277, no. 5693 (January 18, 1979): 175–176, doi:10.1038/277175b0; “Darwin’s Death in South Kensington,” *Nature* 289, no. 5800 (February 26, 1981): 735–735, doi:10.1038/289735a0; Colin Patterson, “Darwin’s Survival,” *Nature* 290, no. 5802 (March 12, 1981): 82–83, doi:10.1038/290082b0.
45. “Darwin’s Death in South Kensington,” *Nature* 289, no. 5800 (February 26, 1981): 735–735, doi:10.1038/289735a0.
46. Keith Thompson, “A radical look at fish tetrapod relationships,” *Paleobiology* 7 (1981): 153–156; see Jeffery W. Pollard, ed., *Evolutionary Theory: Paths into the Future* (New York: Wiley, 1984), particularly Don E. Rosen’s comments on p. 96.
47. David M. Williams and Malte C. Ebach, *Foundations of Systematics and Biogeography* (New York: Springer, 2008).
48. Motoo Kimura, “Evolutionary rate at the molecular level,” *Nature* 217, no. 5129 (1968): 624–626; “Motoo Kimura,” *Wikipedia*, accessed on August 17, 2015, http://en.wikipedia.org/wiki/Motoo_Kimura.
49. One of the few pleasing outcomes of the publication of *Evolution: A Theory in Crisis* (in the midst of sea of outrage) was an invite to meet Gareth Nelson and Norman Platnick at the American Museum of Natural History in 1987. Another was an invite to dinner with Rupert Riedl, perhaps Europe’s leading structuralist at the time, in Heidelberg in 1987 following an anti-Darwin conference [The International Symposium entitled, Neodarwinistische oder Kybernetische Evolution, Heidelberg, West Germany, July 1987, ed., Schmidt F. (Heidelberg: University of Heidelberg Press, 1988.)] And it was also through *Evolution* that I met and came to know Marcel-Paul Schützenberger (known as Marco to his friends and colleagues) a leading mathematician and one of the leading intellectuals in France who was also a major critic of neo-Darwinism and who as I mention below, was one of the influences which directed me to consider the structuralist view. [See Paul. S. Moorhead and Martin M. Kaplan, Wistar Institute of Anatomy and Biology, *Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution: A Symposium Held at the Wistar Institute of Anatomy and Biology, April 25 and 26, 1966*, (New York: Alan R Liss, 1967).]
50. Charles David Allis, Thomas Jenuwein, Danny Reinberg, and Marie-Laure Caparros, *Epigenetics* (Cold Spring Harbor, NY: Cold Spring Laboratory Press, 2007); Pigliucci and Müller, op. cit., Chapter 7; Eva Jablonka and Marion

- J. Lamb, "Transgenerational Epi-genetic Inheritance," in *Evolution—the Extended Synthesis*, and Chapter 12; Gerd Müller, "Epigenetic Innovation."
51. Stuart A. Kauffman, *The Origins of Order: Self-Organization and Selection in Evolution* (New York: Oxford University Press, 1993) Note that Turing, as long ago as 1952, proposed a self-organizing mechanism capable of generating organic patterns; see Alan Turing, "The chemical basis of morphogenesis," *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 237, no. 641 (August 14, 1952): 37–72.
52. Wagner, *Homology, Genes, and Evolutionary Innovation*, 230.
53. Richard O. Prum and Alan H. Brush, "The Evolutionary Origin and Diversification of Feathers," *Quarterly Review of Biology* 77, no. 3 (September 2002), 261–295, 289, emphasis added. For references cited in the passage, see the original article.
54. Douglas H. Erwin, "Macroevolution Is More than Repeated Rounds of Microevolution," *Evolution and Development* 2, no. 2 (March 2000): 78–84, doi:10.1046/j.1525-142x.2000.00045.x.
55. Eric H. Davidson and Douglas H. Erwin, "Gene Regulatory Networks and the Evolution of Animal Body Plans," *Science* 311, no. 5762 (February 10, 2006): 796–800, doi:10.1126/science.1113832; Douglas H. Erwin and Eric H. Davidson, "The Evolution of Hierarchical Gene Regulatory Networks," *Nature Reviews: Genetics* 10, no. 2 (February 2009): 141–48, doi:10.1038/nrg2499.
56. Jerry A. Coyne, "Comment on 'Gene Regulatory Networks and the Evolution of Animal Body Plans,'" *Science* 313, no. 5788 (August 11, 2006): 761, doi:10.1126/science.1126454.
57. Wagner, *Homology, Genes, and Evolutionary Innovation*, 11, emphasis added.
58. Ibid., 125.
59. See Suzan Mazur, "Scott Gilbert: Evolutionary Mechanisms & Knish," Feb. 18, 2009, <http://www.suzanmazur.com/?p=4>.
60. Pigliucci and Müller, *Evolution: the Extended Synthesis*.
61. Wallace Arthur, *Evolution: A Developmental Approach* (Oxford: Wiley-Blackwell, 2011).
62. Mazur, *The Altenberg* 16; Fodor and Piattelli-Palmarini, *What Darwin Got Wrong*.
63. Fodor and Piattelli-Palmarini, *What Darwin Got Wrong*, 77.
64. Ibid, emphasis added.
65. Ibid., 21.
66. Ibid, emphasis added.
67. Michael Ruse, "Form and Function: Placing Brian Goodwin," in *The Intuitive Way of Knowing: A Tribute to Brian Goodwin*, edited by Chris Chetland, David Lambert, and Craig Millar (Edinburgh: Floris Books, 2013). In an excellent article reviewing and contrasting the structuralist functionalist paradigms, Ruse confesses his adherence to functionalism.
68. Jerry A. Coyne, *Why Evolution Is True* (New York: Oxford University Press, 2009).
69. Daniel Dennett, *Darwin's Dangerous Idea: Evolution and the Meanings of Life* (New York: Simon & Schuster, 1995).
70. Richard Dawkins, *The Blind Watchmaker*, new edition (London: Penguin, 2006).
71. John Burdon Sanderson Haldane, "The Cost of Natural Selection," *J. Genetics* 55 (1957): 511–524.
72. Sahotra Sarkar, "The Genomic Challenge to Adaptationism," *The British Journal for the Philosophy of Science*, Epub ahead of print (July 3, 2014), doi:10.1093/bjps/axu002;10.1073: "While adaptationist 'just so' stories have been offered (as typically occurs in every area of biology), recent theoretical analyses based on mathematical

population genetics strongly suggest that non-adaptive processes dominate genome architecture evolution.”

73. Peter B. Becker, ed., “A User’s Guide to the Encyclopedia of DNA Elements (ENCODE),” The ENCODE Project Consortium, *PLoS Biology* 9, no. 4 (2011): e1001046, doi:10.1371/ journal.pbio.1001046; Manolis Kellis, Barbara Wold, Michael P. Snyder, Bradley E. Bernstein, Anshul Kundaje, Georgi K. Marinov, Lucas D. Ward, et al., “Defining Functional DNA Elements in the Human Genome,” *Proceedings of the National Academy of Sciences* 111, no. 17 (April 29, 2014): 6131–6138, doi:10.1073/pnas.1318948111.
74. See Shi Huang, “Inverse Relationship between Genetic Diversity and Epigenetic Complexity,” *Nature Precedings* (January 15, 2009), doi:10.1038/npre.2009.1751.2; Shi Huang, “The Genetic Equidistance Result of Molecular Evolution is Independent of Mutation Rates,” *J Comput Sci Syst Biol.* 1 (December 26, 2008): 92–102; T.Hu, M. Long, D. Yuan, Z. Zhu, Y. Huang, and S. Huang, “The genetic equidistance result: misreading by the molecular clock and neutral theory and reinterpretation nearly half of a century later,” *Sci China Life Sci*, 56 (2013): 254–261.
75. Thomas Nagel, *Mind and Cosmos: Why the Materialist Neo-Darwinian Conception of Nature Is Almost Certainly False* (New York: Oxford University Press, 2012).
76. See Stephen C. Meyer, *Signature in the Cell: DNA and the Evidence for Intelligent Design* (New York: HarperOne, 2009) and the following posts: Jonathan M., “Two of the World’s Leading Experts on Bacterial Flagellar Assembly Take on Michael Behe,” *Evolution News and Views*, March 8, 2013 http://www.evolutionnews.org/2013/03/kelly_hughes_an069881.html; Jonathan M., “ATP Synthase, an Energy-Generating Rotary Motor Engine,” *Evolution News and Views*, May 15, 2013, http://www.evolution-news.org/2013/05/ATP_synthase_an_1072101.html; Jonathan M., “The Eukaryotic Cell Cycle: A Masterpiece of Design,” *Evolution News and Views*, May 30, 2013, http://www.evolutionnews.org/2013/05/the_eukaryotic072631.html; Jonathan M., “Unwinding the Double Helix: Meet DNA Helicase,” *Evolution News and Views*, February 20, 2013 http://www.evolutionnews.org/2013/02/unwinding_the_d_1069371.html.
77. Massimo Pigliucci, “An Extended Synthesis for Evolutionary Biology,” *Annals of the New York Academy of Sciences* 1168, no. 1 (June 2009): 218–228, 218, doi:10.1111/j.1749-6632.2009.04578.x, emphasis added.
78. Ironically, Owen clearly saw Darwin’s project as speculative and premature as he pointed out in his famous review of Darwin’s *Origin* for the *Edinburgh Review*: “The natural phenomena already possessed by science are far from being exhausted... on which the production of species by law might be based.” Richard Owen, “Darwin on the Origin of Species,” *Edinburgh Review* 3 (1860): 487–532; also see Rupke, *Richard Owen: Biology without Darwin*, Chapter 5.
79. On page 796 of *Anatomy of Vertebrates* Owen comments: “No one can enter the ‘saddling ground’ at Epsom, before the start for the ‘Derby,’ without feeling that the glossy-coated, proudly stepping creatures led out before him are the most perfect and beautiful quad-rupeds. As such, I believe the horse to have been predestined and prepared for Man. It may be weakness; but, if so, it is a glorious one, to discern, however dimly, across our finite prison wall, evidence of the ‘Divinity that shapes our ends.’”

Chapter 2—Galápagos

1. Jonathan Weiner, *The Beak of the Finch* (New York: Knopf, 1994), 4. Weiner continues: “Isaac Newton once wrote, with celebrated modesty, ‘If I have seen further than other men it is by standing upon the shoulder of Giants’... The dark volcanoes of the Galapagos are Darwin’s shoulders.” See also Francis Darwin, *The Life and Letters of Charles Darwin*, vol. 1 (London: John Murray, 1887), 247. “This is shown in the following extract from his Pocket Book for this year (1837): ‘In July opened first note-book on Transmutation of Species. Had been greatly struck from about the month of previous March on character of South American fossils, and species on Galapagos Archipelago. These facts (especially latter), origin of all my views.’” Text online at <https://archive.org/stream/LifeAndLettersOfCharlesDarwinV.1/LifeDarwin1#page/n1/mode/2up>.
2. Stephen Jay Gould, *The Structure of Evolutionary Theory* [henceforth, *SET*] (Cambridge, MA: Belknap Press [Harvard], 2002), 109–111.
3. Ibid.

4. Akie Sato, Colm O'hUigin, Felipe Figueroa, Peter R. Grant, B. Rosemary Grant, Herbert Tichy, and Jan Klein, "Phylogeny of Darwin's finches as revealed by mtDNA sequences," *PNAS USA* 96, no. 9 (1999): 5101–5106.
5. Weiner, *The Beak of the Finch*, 17.
6. Ibid. "Cactus finches... nest in cactus; they sleep in cactus; they often copulate in cactus; they drink cactus nectar; they eat cactus flowers; cactus pollen and cactus seeds... Another, the vampire finch ... perches on the back of boobies, pecks at their wings and tails, draws blood and drinks it... There is a vegetarian species that knows how to strip the bark off twigs into long curling ribbons like Geppetto's shavings, to get at the cambium and phloem. There are also species that perch on the backs of iguanas and rid them of ticks. The iguana invites a finch to perch by assuming a posture that makes it look like a cat that wants to be petted."
7. Charles Darwin, *Voyage of the Beagle* (1845 edition), Chapter 17, 402.
8. Letter from Darwin to J. D. Hooker, January 11, 1844, *Darwin Correspondence Project*, University of Cambridge, 2015, <https://www.darwinproject.ac.uk/letter/entry-729>.
9. Weiner, *The Beak of the Finch*; Peter R. Grant and B. Rosemary Grant, *How and Why Species Multiply: The Radiation of Darwin's Finches* (Princeton: Princeton University Press, 2008).
10. The core of Darwin's theory of evolution by natural selection is in essence simple and very easy to grasp. In a widely cited passage in Chapter 4 of the *Origin*, Darwin summarized the core of his argument: "If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organization, and I think this cannot be disputed; if there be, owing to the high geometric powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to the conditions of their existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterized. This principle of preservation, I have called, for the sake of brevity, Natural Selection." [*On The Origin of Species* (London: John Murray, 1859), 126–127.]
11. Darwin got things mostly right but he was not clear as to some of the details regarding the mechanism of speciation. He was unclear, for example, how two varieties occupying the same area could become reproductively isolated. The answer is the 'Wallace Effect,' first proposed in Wallace's *Darwinism* in 1889 [Alfred Russel Wallace, *Darwinism—an Exposition of the Theory of Natural Selection—with Some of Its Applications* (London: Forgotten Books, 2012), Chapter 7, 272.] Wallace speculated rightly that natural selection contributes to reproductive isolation by encouraging (as explained in a recent post): "Diverging populations to stop mating. Each population will have adaptations which increase its fitness in a local environment; matings between individuals of the two different populations will jumble up these adaptations with the result that the offspring cannot compete with individuals from either population; so the mixed offspring have decreased fitness. Now if an individual of one population were to breed with one from the other, they will have less successful young than if they mate within their own population. So natural selection acts to favor either behavioral or morphological mechanisms to prevent mixing, over time the two populations become reproductively isolated and form two species." [Stephen Montgomery, "Speciation: The Origin of Species" *Charles Darwin & Evolution*, Christ's College, Cambridge, 2009, <http://darwin200.christs.cam.ac.uk/node/78>.] That the Wallace Effect applies to the Galápagos finches has been firmly established by the research of the Grants. See Peter and Rosemary Grant, *How and Why Species Multiply: The Radiation of Darwin's Finches* (Princeton: Princeton University Press, 2011).
12. Bailey D. McKay, and Robert M. Zink, "Sisyphean Evolution in Darwin's Finches: Sisyphean Evolution in Darwin's Finches." *Biological Reviews* 90, no. 3 (August 2015): 689–98, doi:10.1111/brv.12127; see also http://www.explore evolution.com/exploreEvolutionFurtherDebate/2009/02/misrepresenting_the_galapagos_1.php.
13. Arhat Abzhanov et al., "Bmp4 and Morphological Variation of Beaks in Darwin's Finches," *Science* 305, no. 5689 (September 3, 2004): 1462–1465, doi:10.1126/science.1098095; Arhat Abzhanov, Winston P. Kuo, Christine Hartmann, Rosemary Grant, Peter R. Grant, and Clifford J. Tabin, "The Calmodulin Pathway and Evolution of Elongated Beak Morphology in Darwin's Finches," *Nature* 442, no. 7102 (August 3, 2006): 563–567,

doi:10.1038/nature04843; Ping Wu, Ting-Xin Jiang, Jen-Yee Shen, Randall Bruce Wideltz, and Cheng-Ming Chuong, “Morphoregulation of Avian Beaks: Comparative Mapping of Growth Zone Activities and Morphological Evolution,” *Developmental Dynamics: An Official Publication of the American Association of Anatomists* 235, no. 5 (May 2006): 1400–1412, doi:10.1002/dvdy.20825.

14. Denton, *Evolution: A Theory in Crisis*, Chapter 4.

15. Darwin, *Origin of Species*, 6th ed. (London: John Murray 1872), 134.

16. *Ibid.*, 84.

17. *Ibid.*, 413–414.

18. *Ibid.*, 146.

19. On reading the *Origin*, Thomas H. Huxley cautioned against Darwin’s stress on such an intensely gradualistic approach [“Huxley, T. H. to Darwin, C. R., Nov. 23, 1859,” *Darwin Correspondence Project*, University of Cambridge, 2015, <http://www.darwinproject.ac.uk/letter/entry-2544>]; on many occasions in the *Origin*, Darwin stressed that evolution by natural selection is an extremely gradual process [1872: 114, 146, 156, 413–414]. He several times used the Latin aphorism *Natura non facit saltum* [1872: 156, 166, 234, 414].

20. Darwin, *Origin of Species* (1872), 23.

21. *Ibid.*, 407.

22. *Ibid.*, 266.

23. Gould, *SET*, 140, emphasis added.

24. *Ibid.*, 141, 143.

25. *Ibid.*, 150, emphasis added.

26. *Ibid.*, 1027–1028.

27. Jonathan B. Edelman and Michael J. Denton, “The Uniqueness of Biological Self-Organization: Challenging the Darwinian Paradigm,” *Biology & Philosophy* 22, no. 4 (December 13, 2006): 579–601, 583, doi:10.1007/s10539-006-9055-5, internal citations omitted.

28. Richard Dawkins, *The Blind Watchmaker*.

29. Daniel Dennett, *Darwin’s Dangerous Idea: Evolution and the Meanings of Life* (New York: Simon & Schuster, 1995), 21.

30. Ernst Mayr, “Darwin’s Influence on Modern Thought,” *Scientific American* (July 2000): 79–83.

31. Dawkins, *Blind Watchmaker*.

32. Mark Ryland, “Applying Natural Philosophy to a Modern Controversy: The Surprisingly Difficult Case of Darwinism, Transformism, and Intelligent Design,” draft version 0.95 (July 2007) (substantially revised version of paper originally presented at the meeting of the American Maritain Association, November 2, 2006): “The standard, reductionist understanding of neo-Darwinian theory treats the obvious teleology of living things to be probably a complete illusion and at best a kind of basically inexplicable epiphenomenon true only of living things —“teleonomy” in the compromising word promoted by Ernst Mayr and others. It is this profound disconnect between our common experience of the purposive world of living beings and a reductionist, a-teleological theory that underlies the continuing doubts about the adequacy and completeness of neo-Darwinism. Indeed, the disconnect is worse than that: unlike most modern sciences, which explain via a-teleological ‘laws’ alone, neo-Darwinism explains *primarily* by chance. Thus, more than a-teleological (the normal status of Newtonian explanations) neo-Darwinism is *anti*-teleological due to the crucial—and relatively unique among modern sciences—role of chance as the basis for all innovation and “progress” in evolution: after all, the fittest must first “arrive” before they can “survive,” and the “arrival of the fittest” is purely a chance event. Natural selection only comes into play as a winnowing process among already existing and reproducing biological entities.”

33. Ernst Mayr, “Darwin’s Influence on Modern Thought,” 80.

34. Mary P. Winsor, *Starfish, Jellyfish, and the Order of Life* (New Haven: Yale University Press, 1976); Edward Stuart Russell, *Form and Function* (London: Murray, 1916); Ronald Amundson, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo* (Cambridge: Cambridge University Press, 2005).
35. Dennett, *Darwin's Dangerous Idea*, 73-77.
36. Gould, *SET*, Chapter 4, 272.
37. Louis Agassiz, *Essay on Classification* (Mineola: Dover, 2004), 9.
38. Richard Owen, *On the Anatomy of Vertebrates*, vol. 3 (London: Longmans, Green and Co., 1866), 796.
39. Nicolaas Adrianus Rupke, *Richard Owen: Biology without Darwin* (Chicago: University of Chicago Press, 2009), Chapter 5, 141.
40. Richard Owen, *On the Anatomy of Vertebrates, Vol. I: Fishes and Reptiles* (London: Longmans, Green, and Co., 1866), v-vi.
41. Dennett, *Darwin's Dangerous Idea*, 20.
42. Dawkins, *Blind Watchmaker*, xvii.
43. Denton, *Evolution: A Theory in Crisis*, Chapter 4, page 92.
44. For micro-evolution on Hawaii see Steve Olson, *Evolution in Hawaii: A Supplement to Teaching About Evolution and the Nature of Science* (Washington, D.C.: National Academies Press, 2004), http://www.nap.edu/openbook.php?record_id=10865&page=1.

Chapter 3—The Hierarchy of Nature

1. See Chapters Five and Six of *Evolution: A Theory in Crisis* (Chevy Chase, MD: Adler & Adler Publishers, 1986); Michael J. Denton, "The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism," *BIO-Complexity* 2013, no. 3 (February 25, 2013): doi:10.5048/BIO-C.2013.3; Mary P. Winsor, *Starfish, Jellyfish, and the Order of Life* (New Haven: Yale University Press, 1976). As I wrote in my *Bio-Complexity* paper: "Although the causal foundation of this remarkable hierarchy was unknown (and still is today), it was widely assumed in the early 19th century that it was an immanent feature of nature and part of the eternal order of the world... Just as Newton had provided a causal explanation for the regularities in the motions of the planets described by Kepler, so biology would eventually have its Newton who would provide a scientific explanation for the hierarchic pattern of nature." [Denton, "The Types: A persistent Challenge to Darwinian Pan-Selectionism."] As Winsor comments: "Many biologists seemed to feel that although their field was not yet as exact, coherent and logical as Newtonian science, it had the potential of becoming so... The role of a scientist was to discover within the confusing diversity of living things the underlying order and lawfulness." [Winsor, *Starfish, Jellyfish, and the Order of Life*, 4-5.]
2. Edward Stuart Russell, *Form and Function* (London: Murray, 1916), 241; see also Winsor, *Starfish, Jellyfish, and the Order of Life*, Chapter 4; and Ronald Amundson, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo* (Cambridge: Cambridge University Press, 2005), Chapter 2. See also my above-cited "The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism." As Winsor points out [Winsor, *Starfish, Jellyfish, and the Order of Life*, Chapter 4], the concept that life's hierarchic pattern is inherently lawful was witnessed in the attempt of early nineteenth century taxonomists to organize classification schemes in terms of geometric and numeric patterns such as the circular-quinarian system of William Sharp Macleay and Swainson. Even Huxley was attracted to these orderly geometric systems. He commented on Macleay's system [cited in Winsor, *Starfish, Jellyfish, and the Order of Life*, 91]: "The circular system appears to me to stand in the same relationship relation to the true theory of animal form as Kepler's Laws to the fundamental doctrine of astronomy. The generalizations of the Circular system are for the most part, true, but they are empirical, not ultimate laws... The laws of the similarity and variation of development of Animal form are yet required to explain the circular theory." Huxley's attraction to Macleay's system serves to underline further that the core aim of early nineteenth century biology was to find lawful explanations of the biological realm. As Winsor comments: "He had not found the answer,

biology's law of gravity, but he was searching in that direction." [Winsor, *Starfish, Jellyfish, and the Order of Life*, 91.] However anomalous it may seem in the context of today's biology, profoundly wedded as it is to functionalist notions and the concept of life's forms as ultimately contingent the belief that the order of life is immanent in the fabric of things was the very *Zeitgeist* of early nineteenth-century biology. See also Dov Ospovat, *The Development of Darwin's Theory: Natural history, Natural Theology, and Natural Selection, 1838-1859* (Cambridge: Cambridge University Press, 1995), Chapter 1.

3. Mary Winsor, "The Creation of the Essentialism Story: An Exercise in Metahistory," *History and Philosophy of the Life Sciences* 28 (2006): 149-174.
4. Amundson, *The Changing Role of the Embryo in Evolutionary Thought*, 11. Later in the book (100-101), Amundson makes an intriguing observation by showing how the advocates of the historiography tried to play down Owen's contributions in refuting what Amundson termed teleological finalism (pan adaptationism).
5. Ibid., 18.
6. Ibid., 62.
7. Hans Jonas, *The Phenomenon of Life: Toward a Philosophical Biology* (Evanston, IL: Northwestern University Press, 2001), 94-95.
8. The term *Bauplan* generally refers to the novel ground plans of the major Types—such as the body plans of the different phyla or main classes of organisms such as insects as well as complex homologs like the pentadactyl limb or angiosperm flower. *Bauplans* generally consist of a suite of individual taxa-defining novel homologs. The *Bauplan* of the cell includes several novel homologs, the genetic code, the ribosome, the cell membrane and the core metabolic pathways etc. The *Bauplan* of the flower consists again of a suite of novel homologs including sepals, petals, and so forth.
9. Rupert Riedl, "A Systems-Analytical Approach to Macro-Evolutionary Phenomena," *Quarterly Review of Biology* 52, no. 4 (1977): 351-370.
10. There is controversy about whether there are "reptiles" with pennaceous feathers. Some researchers have argued that they are actually secondarily flightless birds and NOT reptiles/dinosaurs. For references see Casey Luskin, "Is the Latest 'Feathered Dinosaur' Actually a Secondarily Flightless Bird?," *Evolution News & Views*, Nov. 12, 2008, http://www.evolutionnews.org/2008/11/is_the_latest_feathered_dinosa013131.html.
11. "Dinosaur," *Wikipedia*, accessed on August 18, 2015, <http://en.wikipedia.org/wiki/Dinosaur>.
12. Penelope J. Gullan and Peter S. Cranston, *The Insects: An Outline of Entomology*, 4th ed. (Chichester, West Sussex: Wiley-Blackwell, 2010), section 2.42, page 46.
13. Louis P. Ronse De Craene, *Floral Diagrams: An Aid to Understanding Flower Morphology and Evolution* (Cambridge; New York: Cambridge University Press, 2010).
14. Ramin Yadegari and Gary N. Drews, "Female Gametophyte Development," *The Plant Cell* 16, no. suppl. 1 (June 2004): S133-S141, doi:10.1105/tpc.018192; Valayamghat Raghavan, "Some Reflections on Double Fertilization, from Its Discovery to the Present: Tansley Review," *New Phytologist* 159, no. 3 (July 25, 2003): 565-583, doi:10.1046/j.1469-8137.2003.00846.x.
15. See Dr. Larry Jensen's video, "Mitochondria," "Reproductive Cycle of Flower Plants/The Amazing Lives of Plants," online video clip, YouTube, published by McGraw-Hill (2003) web, http://www.youtube.com/watch?v=0UEpq1W9C_E; Ramin Yadegari and Gary N. Drews, "Female Gametophyte Development," *The Plant Cell Online* 16, no. suppl_1 (March 12, 2004): S133-S141, doi:10.1105/tpc.018192.
16. Denton, *Evolution: A Theory in Crisis*, Chapter 5; "Mammal," *Wikipedia*, accessed on August 18, 2015, <https://en.wikipedia.org/wiki/Mammal>; for the six layers of the cortex see Korbinian Brodmann, and Laurence J. Gary, *Brodmann's Localization in the Cerebral Cortex: The Principles of Comparative Localisation in the Cerebral Cortex Based on Cytoarchitectonics* (New York: Springer, 2006), Chapter 1, 33; For a list of mammalian characters, see Günter P. Wagner, *Homology, Genes, and Evolutionary Innovation* (Princeton: Princeton University Press, 2014)

table 4.1, 128.

17. Irma Varela-Lasheras, Alexander J. Bakker, Steven D. van der Mije, Johan A. J. Metz, Joris van Alphen, and Frietson Galis, "Breaking Evolutionary and Pleiotropic Constraints in Mammals: On Sloths, Manatees and Homeotic Mutations," *EvoDevo* 2 (2011): 11, doi:10.1186/2041-9139-2-11.
18. "Dentition," *Wikipedia*, accessed on August 18, 2015, <https://en.wikipedia.org/wiki/Dentition>.
19. Brooke A. Armfield, Zhengui Zheng, Sunil Bajpai, Christopher J. Vinyard, and JGM Thewissen, "Development and Evolution of the Unique Cetacean Dentition," *PeerJ* 1 (February 19, 2013): e24, doi:10.7717/peerj.24.
20. Wallace Arthur, *Evolution: A Developmental Approach* (Chichester, West Sussex: Wiley-Blackwell, 2011), Chapter 13. See section titled "Centipede Segments."
21. *Ibid.*, Chapter 9, see section 9.4
22. Gregory D. Edgecombe and Gonzalo Giribet. "Evolutionary Biology of Centipedes (Myriapoda: Chilopoda)" *Annual Review of Entomology* 52, no. 1 (January 2007): 151– 170, doi:10.1146/annurev.ento.52.110405.091326.
23. The name "coleoptera" (shield-wing) was given by Aristotle for the hardened shield-like forewings.
24. Owain Westmacott Richard, and Richard Gareth Davies, *Imms' General Textbook of Entomology*, vol. 2., 10th ed. (London: Chapman and Hall, 1977), 816.
25. David R. Maddison, "Coleoptera," *Tree of Life web project*, September 11, 2000, <http://tolweb.org/Coleoptera/8221>.
26. Olivier Béthoux, "The Earliest Beetle Identified," *Journal of Paleontology* 83, no. 6 (November 2, 2009): 931–937. doi:10.1666/08-158.1.
27. Richard and Davies, *Imms' General Textbook of Entomology*, 1234.
28. Christian Rabeling, Jeremy M. Brown, and Manfred Verhaagh. "Newly Discovered Sister Lineage Sheds Light on Early Ant Evolution," *Proceedings of the National Academy of Sciences* 105, no. 39 (September 30, 2008): 14913–14917. doi:10.1073/pnas.0806187105.
29. Edward O. Wilson and Bert Hölldobler, *The Ants* (Boston: Harvard University Press), Chapter 2.
30. Sean Carroll, *Endless Forms Most Beautiful: The New Science of Evo Devo and the Making of the Animal Kingdom* (New York: W. W. Norton & Co., 2006), 201, fig. 8.2; "Nymphalidae," *Wikipedia*, accessed on August 18, 2015, <http://en.wikipedia.org/wiki/Nymphalidae>.
31. Noam Chomsky, *The Science of Language: Interviews with James McGilvray* (New York: Cambridge University Press, 2012).
32. Jerry Coyne, "Bill Nye Won Last Night's Creationism Debate," *The New Republic*, February 5, 2014, <http://www.newrepublic.com/article/116478/bill-nye-ken-ham-debate-creationism-and-evolution-science-wins>; see also Coyne's *Why Evolution Is True* (New York: Viking Penguin, 2009).
33. Jerry Coyne, *Why Evolution Is True* (New York: Oxford University Press, 2009).
34. Stephen Jay Gould, *The Panda's Thumb: More Reflections in Natural History* (New York: Norton, 1992), 189; Gould, "Evolution's Erratic Pace," *Natural History* 86, no. 5 (May 1977): 14.
35. Riedl, "A Systems-Analytical Approach to Macro- Evolutionary Phenomena," 351–370, 354.
36. John Beatty, "Classes and Cladists," *Systematic Zoology* 31, no. 1 (March 1982): 25–34, emphasis added, accessible from <http://www.jstor.org/discover/10.2307/2413411?uid=3739136&uid=2129&uid=2&uid=70&uid=4&sid=21104215743803>.
37. See discussion in Chapter 6, section 6.1.
38. Riedl, "A Systems-Analytical Approach to Macro- Evolutionary Phenomena," 351–370.

39. Gould, *SET*, 1065, emphasis added.
40. Norman I. Platnick, "Defining Characters and Evolutionary Groups," *Systematic Zoology* 31, no. 3 (September 1982): 282–284, 282, accessible from <http://www.jstor.org/discover/10.2307/2413233?uid=3739136&uid=2&uid=4&sid=21104215660463>.
41. Gareth Nelson and Norman Platnick, *Systematics and Biogeography* (New York: Columbia University Press, 1981), 328, emphasis added. See also Denton, *Evolution: A Theory in Crisis*, chapter 5.
42. The Natural History Museum in South Kensington in the UK and the American Museum of Natural History in NY.
43. As already mentioned in Chapter 1, for a review of the many controversies that surrounded the "rise of cladism" in the 1980s and 1990s, see David Williams, *Foundations of Systematics and Biogeography* (New York: Springer, 2008), Chapter 6.
44. Charles Darwin, *Origin of Species*, 6th ed. (London: John Murray 1872), 264 (Chapter 10): "The distinctness of specific forms, and their not being blended together by innumerable transitional links, is a very obvious difficulty."
45. Penny Higgins, "Use and Abuse of the Fossil Record: Defining Terms," *Skeptical Inquirer*, The Committee for Skeptical Inquiry, September 9, 2006 http://www.csicop.org/specialarticles/show/use_and_abuse_of_the_fossil_record_defining_terms.
46. Wallace Arthur, "Intraspecific Variation in Developmental Characters: The Origin of Evolutionary Novelty," *American Zoologist* 40 (2000): 811–818.
47. Carroll, *Endless Forms Most Beautiful*, Chapter 11.
48. Ernst Mayr, "The Emergence of Evolutionary Novelty," in S. Tax, ed., *Evolution After Darwin* (Chicago: Chicago University Press, 1959), vol. 1, 349–380. Available online: http://archive.org/stream/evolutionafterda01taxs/evolutionafterda01taxs_djvu.txt. Mayr defines novelty (p. 351) as: "any newly arisen character, structural or otherwise, that differs more than quantitatively from the character that gave rise to it... Tentatively, one might restrict the designation 'evolutionary novelty' to any newly acquired structure or property that permits the assumption of a new function." He advocated exaptation as a major route to novelty (p. 377): "The emergence of new structures is normally due to the acquisition of a new function by an existing structure."
49. For examples, see: Matthew H. Nitecki, ed., *Evolutionary Innovations* (Chicago: University of Chicago Press, 1990); Arthur, "Intraspecific Variation in Developmental Characters: The Origin of Evolutionary Novelty," 811–818; Günter P. Wagner, "What Is the Promise of Developmental Evolution? Part I: Why Is Developmental Biology Necessary to Explain Evolutionary Innovations?" *Journal of Experimental Zoology* 288, no. 2 (August 15, 2000): 95–98, doi:10.1002/1097-010X(20000815)288:2<95::AID-JEZ1>3.0.CO;2-5; Alan C. Love, "Evolutionary Morphology, Innovation, and the Synthesis of Evolutionary and Developmental Biology," *Biology and Philosophy* 18, no. 2 (2003): 309–345; Richard O. Prum, "Evolution of the Morphological Innovations of Feathers," *Journal of Experimental Zoology* 304B, no. 6 (2005): 570–579; Gerd B. Müller and Stuart A. Newman, "The Innovation Triad: An EvoDevo Agenda," *Journal of Experimental Zoology* 304B, no. 6 (2005): 487–503; Massimo Pigliucci, "What, If Anything, Is an Evolutionary Novelty?" *Philosophy of Science* 75, no. 5 (December 2008): 887–898, doi:10.1086/594532. See also Günter P. Wagner and Vincent J. Lynch, "Evolutionary Novelty," *Current Biology* 20 (2010): R48–52. Wagner and Lynch describe a novelty as: "A novel body part that is neither homologous to any body part in the ancestral lineage nor serially homologous to any other body part of the same organism. To define novelty using the homology concept may sound like replacing one poorly defined term by another. In recent years, however, homology has re-emerged as a core organizing principle in evolutionary developmental biology. Applied to morphological structures the term homology, refers to quasi-independent, individualized body parts that have their own evolutionary history, i.e., are derived from the same body part in a common ancestor and which form lineages of descent with modification, as exemplified by the evolutionary history of tetrapod limbs and eyes." For further examples, see Richard O. Prum and Alan H. Brush, who write of "many novelties involved in feather evolution" in their "The Evolutionary Origin and Diversification of Feathers," *The Quarterly Review of Biology* 77, no. 3 (September 2002): 261–295; Gerd B. Müller and Günter P. Wagner "Novelty in Evolution: Restructuring the Concept," *Annual Review of Ecology and Systematics* 22 (1991): 229–256; Mary Jane West-Eberhard, who in

Developmental Plasticity and Evolution (Oxford University Press, 2003) defines a novel trait as “a novel trait [based on] a qualitatively distinct developmental variant” (page 198); Andreas Wagner, *The Origins of Evolutionary Innovations: A Theory of Transformative Change in Living Systems* (New York: Oxford University Press, 2011). The recently published book by Wagner, *Homology, Genes, and Evolutionary Innovation* contains several chapters (e.g., Chapter 4) devoted to defining evolutionary novelties.

50. Pigliucci, “What, If Anything, Is an Evolutionary Novelty?” 888.
51. Wagner, *Homology, Genes, and Evolutionary Innovation*, Chapter 4, 126.
52. A recent series of papers in the *Journal of Experimental Zoology* was devoted entirely to the problem of evolutionary novelties and how they arise. See “Special Issue: Perspectives on Evolutionary Novelty and Evo-Devo,” *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 318, no. 6 (September 2012): 417–517.
53. Günter P. Wagner, “What Is the Promise of Developmental Evolution? Part I: Why Is Developmental Biology Necessary to Explain Evolutionary Innovations?” 95.
54. Wagner and Lynch, “Evolutionary Novelties,” R48.-R49.
55. Vincent J. Lynch, Robert D. Leclerc, Gemma May, and Günter P. Wagner, “Transposon-Mediated Rewiring of Gene Regulatory Networks Contributed to the Evolution of Pregnancy in Mammals,” *Nature Genetics* 43, no. 11 (September 25, 2011): 1154–1159, 1154, doi:10.1038/ng.917.
56. Pigliucci, “What, If Anything, Is an Evolutionary Novelty?” 887, emphasis added.
57. Denton, *Evolution: A Theory in Crisis*, 155.
58. Darwin, *Origin of Species* (1872), 264 (Chapter 10).

Chapter 4—Non-Adaptive Order

1. “Darwin’s Statue on the move,” Natural History Museum, May 23, 2008, September 27, 2014, *Internet Archive*, <https://web.archive.org/web/20140927214551/http://www.nhm.ac.uk/about-us/news/2008/may/darwins-statue-on-the-move13846.html>, accessed August 17, 2015.
2. Charles Darwin, *On the Origin of Species* (London: John Murray, 1872), 2 (Introduction).
3. For a definition of non-adaptive see beginning of Chapter 1.
4. Stephen Jay Gould, *The Structure of Evolutionary Theory* (Cambridge, MA: Belknap Press [Harvard], 2002), 252; henceforth cited as Gould, *SET*.
5. The full text of *On the Nature of Limbs* is available at <https://archive.org/details/Owen1849br46D>.
6. Richard Owen, *On the Nature of Limbs* (London: John Van Voorst, 1849), 1.
7. David M. Williams, *Foundation of Systematics and Biogeography* (New York: Springer, 2008). In the foreword Gareth Nelson laments the dismissal of the thinking of Goethe and other pre-Hennigian morphologists.
8. Rupert Riedl, *Order in Living Organisms* (New York: John Wiley and Son’s, 1978), xv.
9. Ron H. Brady, “Form and Cause in Goethe’s morphology,” in Francis J. Zucker, Harvey Wheeler, and Frederick Amrine eds., *Goethe and the Sciences: A Reappraisal*, Boston Studies in the Philosophy of Science vol. 97, edited by S. Cohen and Marx W. Wartofsky (Dordrecht: D. Reidel Publishing Company, 1987), 257-300.
10. Owen, *On the Nature of Limbs*, 9. It is important to stress again, as mentioned in the Introduction, that despite their focus on the apparently abstract homologous patterns which define the Types, neither Owen, as is obvious in *Limbs*, nor any of the other pre-Darwinian typologists denied the fact of adaptation or its significance [Gould, *SET*, 324.] Instead, they saw adaptation to be a secondary, peripheral phenomena, the result not of internal constraints or natural law (order from within), but as a response to environmental conditions (satisfying an external order from without).

As Russell points out, Haeckel for example distinguished [Russell, *Form and Function* (London: Murray, 1916), 248]: “The internal *Bildungstrieb* [formative force]... the mechanical effect of the material structure of the *crystal* or the germ, and adaptation, or the external *Bildungstrieb*, [which he saw as] modifications induced by the environment.” Goethe’s view was similar. [Gould, *SET*, 289-290.] Environmental adaptation was also seen by H. G. Bronn as one of the major causal factors shaping organic form. [Russell, *Form and Function*, 203.]

11. Ronald Amundson, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo* (Cambridge: Cambridge University Press, 2005), 93.
12. Ibid., 9–10.
13. Ibid., 10.
14. Owen, *On the Nature of Limbs*, 85. Owen is surely right; pan-adaptationalism does indeed arise at least partially from the fallacy of accepting the machine analogy. Machines such as a watch, Paley’s watch, are “bundles of adaptations” in which all parts are arranged to serve functions. If the analogy holds, then pan-adaptationism must also hold and organisms must also be bundles of adaptations. But Owen’s jibe, which was aimed specifically at natural theology (which has always emphasized the machine/organism analogy), may also be seen as aimed at Darwinism. Darwinism no less than natural theology sees organisms as machines i.e., contingent assemblages put together not by a Divine Watchmaker but by the Blind Watchmaker, bit by bit, by cumulative selection, to serve various adaptive purposes. Of course, because there is no objective grounds for assuming that organisms are machines, there is no objective reason for holding to the fallacy. If organisms are, as Owen believed (and I concur) at least in part, natural forms, then pan-adaptationalism is ruled out on first principles. And of course, as Owen asserts in the citations above, no human-constructed adaptation or machine is encumbered with constraints analogous to the *Bauplans* that underlie the adaptive diversity of life.
15. Owen, *On the Nature of Limbs*, 40.
16. Darwin, *Origin of Species* (1972), 382.
17. Ibid., 382–383
18. Ibid., 383.
19. Ibid., 384.
20. Owen, *On the Nature of Limbs*, 40.
21. Amundson, *The Changing Role of the Embryo*, 97.
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37. *Ibid.*, 485.
38. *Ibid.*, 116.
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41. Bateson, *Materials for the Study of Variation*, 410.
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44. Thomas Nagel, *Mind and Cosmos: Why the Materialist Neo-Darwinian Conception of Nature Is Almost Certainly False* (New York: Oxford, 2012), Chapter 6, 126.
45. However, note that Darwin was aware that some cases of non-adaptive order might not be ancient adaptations but might be what Gould (*SET*, Chapter 11) refers to as “spandrels.” In Darwin’s words (*Origin of Species* [1872], 9): “if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation.”
46. Darwin, *Origin of Species* (1872), 160.
47. *Ibid.*, 383, emphasis added.
48. Darwin concurred with Owen regarding the non-adaptive nature of the homologs, see Amundson, *The Changing Role of the Embryo*, 100–101.
49. Nor has anyone else ever shown that the identical design of the three pairs of insect limbs, or the two pairs of wings rather than one attached to the second and third segments of the insect thorax, or the constraint of no more than eleven abdominal segments, or any other defining homologs of the insects were adaptive in the “ancestral” insect. (Note: Some insects get by with one pair of wings. Beetles fly with one pair of wings and bees hook their wings together into a single aerofoil.)
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51. Denton, “The Types: A Persistent Structuralist Challenge to Darwinian Functionalism.” The D’Arcy Thompson quote is from *On Growth and Form*, (Cambridge: Macmillan, 1945), 873.
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Chapter 5—Evo-Devo

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Chapter 6—The Tree of Life and Distinctive Types

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[14.](#) Riedl, “A Systems-Analytical Approach to Macro- Evolutionary Phenomena” 354.

[15.](#) The co-opting of these three skeletal elements for different functions during vertebrate evolution from fish to mammal is shown in all major texts of vertebrate paleontology and evolution.

[16.](#) Phrases such as “the evidence ... does not provide convincing grounds for believing that the phenomenon of life conforms to a continuous pattern” (page 194), “if gradual evolution is true” (page 228), and “Nature has not been reduced to the continuum that the Darwinian model demands” (page 357) do convey the impression of denying evolution and common descent. This was not my intention. I do, however, reject any sort of gradual bit-by-bit evolution, for reasons I am presenting here. I also reject the term “evolution” in the mainstream meaning of the word, i.e., “gradual adaptive change.” The tree of life is not connected by innumerable adaptive pathways leading from the trunk to all the most peripheral twigs.

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Chapter 7—Bridging Gaps: Cells and Proteins

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Chapter 8—Bridging Gaps: Flowering Plants

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Chapter 9—Bridging Gaps: Limbs, Feathers, Wings, and Eels

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42. Denton, *Evolution: A Theory in Crisis*, 209.
43. Richard O. Prum and Alan H. Brush, "The Evolutionary Origin and Diversification of Feathers," *The Quarterly Review of Biology* 77, no. 3 (September 2002): 261–295.
44. Ibid.; Richard O. Prum, "Development and Evolutionary Origin of Feathers," *The Journal of Experimental Zoology* 285, no. 4 (December 15, 1999): 291–306; Richard O. Prum, "Evolution of the Morphological Innovations of Feathers," *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 304B, no. 6 (November 15, 2005): 570–579, doi:10.1002/jez.b.21073; Richard O. Prum and Alan H. Brush, "Which Came First, the Feather or the Bird?" *Scientific American* 288 no. 3 (March 2003): 84–93 [reprinted in *Evolution: A Scientific American Reader* (Chicago: University of Chicago Press, 2006), 213–224].
45. Prum and Brush, "The Evolutionary Origin and Diversification of Feathers," 265. The internal reference is to Walter J. Bock, "The Role of Adaptive Mechanisms in the Origin of Higher Levels of Organization," *Systematic Zoology* 14

(1965): 272–287, emphasis added.

46. Prum and Brush, “Which Came First, the Feather or the Bird?” 86.
47. Matthew P. Harris, P. Scott Williamson, John F. Fallon, Hans Meinhardt, and Richard O. Prum, “Molecular Evidence for an Activator-Inhibitor Mechanism in Development of Embryonic Feather Branching,” *Proceedings of the National Academy of Sciences* 102, no. 33 (August 16, 2005): 11734–11739, doi:10.1073/pnas.0500781102.
48. Prum and Brush, “Which Came First, the Feather or the Bird?” 90.
49. Ibid., 90–91: “The expression of Shh and Bmp2 begins in the feather placode, where the pair of proteins is produced in a polarized anterior-posterior pattern. Next, Shh and Bmp2 are both expressed at the tip of the tubular feather germ during its initial elongation and, following that, in the epithelium that separates the forming barb ridges, establishing a pattern for the growth of the ridges. Then, in pennaceous feathers, Shh and Bmp2 signaling lays down a pattern for helical growth of barb ridges and rachis formation, whereas in plumulaceous feathers the Shh and Bmp2 signals create a simpler pattern of barb growth. Each stage in the development of a feather has a distinct pattern of Shh and Bmp2 signaling. Again and again the two proteins perform critical tasks as the feather unfolds to its final form.”
50. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers.”
51. Ibid., 283.
52. Thor Hanson, *Feathers: The Evolution of a Natural Miracle* (New York: Basic Books, 2011), 56.
53. Ibid., 56.
54. For the frayed-scale theory, see Heilmann, *The Origin of Birds*, and Regal, “The Evolutionary Origin of Feathers,” both cited above.
55. Hanson, *Feathers*, 37.
56. Ibid., 37.
57. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers,” 284.
58. Ibid., 270–275.
59. Gary Ritchison, “BIO 554/754 Ornithology: Feather Evolution,” Eastern Kentucky University, http://people.eku.edu/ritchison/feather_evolution.htm.
60. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers,” 270–275.
61. Ibid. Note: The actual evolutionary stage in which the barbules originated might have before or after the origin of the bipinnate feather (third image in Figure 9-2). In modern feathers the barbs of both pennaceous feathers and of plumaceous feathers have barbules; those of the closed, pennaceous feather are short and interlocked by hooks and grooves on the distal and proximal barbs respectively. Those of the plumaceous feather are “elongate barbules with nodal prongs that interact among barbs to form disorderly tangles that produce a large volume”—a ball of fluff—which has excellent insulating qualities (Prum, “Development and Evolutionary Origin of Feathers,” 293). In whichever order these novelties originated, they are novelties nonetheless!
62. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers,” 287–288, emphasis added and all internal references removed.
63. Ibid. 288; The authors comment: “[so] are the derived mechanisms by which these novel structures develop.” For two videos, showing the development of the parallel barbs of the plumaceous feather (Figure 9-2, second image) and their helical displacement and attachment to the rachis to form the unbranched barbs of the pinnate feather (Figure 9-2, third image), see the web site http://people.eku.edu/ritchison/feather_evolution.htm.
64. Matthew P. Harris, et al., “Molecular Evidence for an Activator-Inhibitor Mechanism in Development of Embryonic Feather Branching.” The authors comment (page 11738–11739): “Here, we provide evidence of the molecular basis of the activation–inhibition mechanism underlying the formation of complex morphologies during vertebrate development. The two- and three-component activator–inhibitor models produce realistic descriptions of the interactions between Shh and Bmp2 expression and barb specification during barb ridge morphogenesis. The empirical data support the activating and inhibitory functions of Shh and Bmp2 assumed in the two-component models. The empirically supported two-component models are sufficient to describe barb morphogenesis in plumulaceous natal chick down, which lack[s] strong D/V polarization and a rachis. The two-component model is

not sufficient to generate the more complex, D/V polarized patterns in Shh and Bmp2 signaling that are observed during barb ridge morphogenesis in pennaceous feathers... But mathematical analyses further predict that Shh and Bmp2 signaling interacts with additional inhibitory and D/V polarized signal gradients in the feather germ to produce the more complicated, and evolutionarily derived, morphology of pennaceous feathers, which is characterized by ventral new barb ridge creation, helical barb ridge growth, and dorsal barb ridge fusion... This integrated view of barb ridge morphogenesis provides previously uncharacterized insights into the evolution of complex, pennaceous feather branching structure from more primitive plumulaceous feather structure... The first branched feather barbs evolved through the establishment of an activator–inhibitor interaction between the plesiomorphic, or preexisting, interacting Shh and Bmp2 signaling systems in the basal epithelium (i.e., marginal plate) of the feather germ to produce meristic patterning and morphogenesis of the barbs. The subsequent plumulaceous-to-pennaceous morphological transition evolved through the derived integration of an additional short-range inhibitor and a D/V polarized signaling gradient. Thus, evolutionary novelty of pennaceous structure required the coupling of the plesiomorphic, previously independent Shh and Bmp2 module and D/V signal gradient. The signaling mechanisms that produce complex barb branching in pennaceous feathers were an inherent potential of the molecular mechanisms previously evolved with the origin of simpler, plumulaceous feathers. Integrated signaling between modular developmental systems provide both stable mechanisms of morphogenesis and inherent capacities for the generation of morphological and evolutionary novelties.”

65. Mingke Yu, Ping Wu, Randall B. Wideltz, and Cheng-Ming Chuong, “The Morpho-genesis of Feathers,” *Nature* 420, no. 6913 (November 21, 2002): 308–312, doi:10.1038/ nature01196.
66. Ibid., abstract.
67. For a discussion of the evo-devo basis of feather individualization, see Wagner, *Homology, Genes, and Evolutionary Innovation*, 323–326.
68. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers,” 289.
69. Hanson, *Feathers*, 38.
70. Prum and Brush, “The Evolutionary Origin and Diversification of Feathers.”
71. Harris et al., “Molecular Evidence for an Activator-Inhibitor Mechanism in Development of Embryonic Feather Branching,” 11739, emphasis added.
72. Alfred R. Wallace, *The World of Life*, see Chapter 14 entitled, “Birds and Insects: As proof of an organizing and directive life principle,” available at, “Chapter XIV,” *Internet Archive*, <https://archive.org/stream/worldoflifemanif00walliala#page/286/mode/2up>.
73. Glenn Jepson, “Bat Origins and Evolution,” *Biology of Bats*, edited by William A. Wimsatt, vol. 1 (New York: Academic Press, 1970), 1–64, see page 54; Denton, *Evolution: A Theory in Crisis*, 216.
74. Jepson, “Bat Origins and Evolution,” 44.
75. Norberto P. Giannini, “Toward an Integrative Theory on the Origin of Bat Flight,” in *Evolutionary History of Bats: Fossils, Molecules, and Morphology*, edited by Gregg F. Gunnell and Nancy B. Simmons (New York: Cambridge University Press, 2012), Chapter 10.
76. Karen E. Sears, Richard R. Behringer, John J. Rasweiler IV, and Lee A. Niswander, “Development of Bat Flight: Morphologic and Molecular Evolution of Bat Wing Digits,” *Proceedings of the National Academy of Sciences* 103, no. 17 (April 25, 2006): 6581–6586, 6581, doi:10.1073/pnas.0509716103.
77. Ibid.
78. Stephen M. Jackson and Richard W. Thorington, Jr., *Gliding Mammals: Taxonomy of Living and Extinct Species* (Washington, DC: Smithsonian Institution Scholarly Press, 2012), 3. PDF is available online at https://repository.si.edu/bitstream/handle/10088/18186/SCZ638_Jackson_FINAL_web.pdf?sequence=1&isAllowed=y.
79. “Flying Squirrel,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Flying_squirrel.
80. “Anomalure,” *Wikipedia*, accessed on September 9, 2015, <http://en.wikipedia.org/wiki/Anomaluridae>.

81. “Colugo,” *Wikipedia*, accessed on September 9, 2015, <http://en.wikipedia.org/wiki/Colugo>.
82. “Volaticotherium,” *Wikipedia*, accessed on September 9, 2015, <http://en.wikipedia.org/wiki/Volaticotherium>.
83. “Flying and gliding animals,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Flying_and_gliding_animals; “Common Gliding Lizard,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Common_Gliding_Lizard.
84. “Flying frog,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Flying_frog.
85. Giannini, “Toward an Integrative Theory on the Origin of Bat Flight.”
86. Mark P. Witton, *Pterosaurs: Natural History, Evolution, Anatomy* (Princeton: Princeton University Press, 2013), Chapter 3, fig. 3.1.
87. *Ibid.*, 13.
88. Giannini, “Toward an Integrative Theory on the Origin of Bat Flight,” 353–354.
89. *Ibid.*, emphasis added.
90. Zhe Wang, Dong Dong, Binghua Ru, Rebecca L. Young, Naijian Han, Tingting Guo, and Shuyi Zhang, “Digital Gene Expression Tag Profiling of Bat Digits Provides Robust Candidates Contributing to Wing Formation,” *BMC Genomics* 11 (2010): 619, doi:10.1186/1471-2164-11-619.
91. *Ibid.*, 8, emphasis added.
92. Carroll, *Endless Forms Most Beautiful*, Chapter 8.
93. Zhe Wang, Mengyao Dai, Yao Wang, Kimberly L. Cooper, Tengting Zhu, Dong Dong, Junpeng Zhang, and Shuyi Zhang, “Unique Expression Patterns of Multiple Key Genes Associated with the Evolution of Mammalian Flight,” from the abstract, *Proceedings of the Royal Society B: Biological Sciences* 281, no. 1783 (2014): 20133133, abstract, doi:10.1098/rspb.2013.3133.
94. The idea that macroevolution cannot be a mere extension of microevolution was promoted vigorously and notoriously by Richard Goldschmidt and is now defended by recent authors. See Chapter 1.
95. Kimberly L. Cooper and Clifford J. Tabin, “Understanding of Bat Wing Evolution Takes Flight,” *Genes & Development* 22, no. 2 (January 15, 2008): 121–124, doi:10.1101/gad.1639108.
96. Sears et al., “Development of Bat Flight: Morphologic and Molecular Evolution of Bat Wing Digits,” 6585, emphasis added.
97. *Ibid.*, the same protein causes slightly increased digit length in rats and mice.
98. Scott D. Weatherbee, Richard R. Behringer, John J. Rasweiler, and Lee A. Niswander, “Interdigital Webbing Retention in Bat Wings Illustrates Genetic Changes Underlying Amniote Limb Diversification,” *Proceedings of the National Academy of Sciences* 103, no. 41 (October 10, 2006): 15103–15107, doi:10.1073/pnas.0604934103. As the authors comment on page 15103: “Strikingly, the retention of interdigital webbing in the bat forelimb is correlated with a unique pattern of *Fgf8* expression in addition to the Bmp inhibitor *Gremlin*. By using a functional assay, we show that maintenance of interdigit tissue in the bat wing depends on the combined effects of high levels of Fgf signaling and inhibition of Bmp signaling. Our data also indicate that although there is not a conserved mechanism for maintaining interdigit tissue across amniotes, the expression in the bat forelimb inter-digits of *Gremlin* and *Fgf8* suggests that these key molecular changes contributed to the evolution of the bat wing.” See also “Bat wing development,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Bat_wing_development.
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100. Giannini, “Toward an Integrative Theory on the Origin of Bat Flight,” 376–377, emphasis added.
101. Kristin L. Bishop, “The Evolution of Flight in Bats: Narrowing the Field of Plausible Hypotheses,” *The Quarterly Review of Biology* 83, no. 2 (June 2008): 153–169.

- [102.](#) Giannini, “Toward an Integrative Theory on the Origin of Bat Flight,” 376–377.
- [103.](#) C. J. Cretekos, Y. Wang, E. D. Green, NISC Comparative Sequencing Program, J. F. Martin, J. J. Rasweiler, and R. R. Behringer, “Regulatory Divergence Modifies Limb Length between Mammals,” *Genes & Development* 22, no. 2 (January 15, 2008): 141–51, 147, doi:10.1101/gad.1620408, emphasis added.
- [104.](#) Freud’s paper on eels, “Beobachtungen über Gestaltung und feineren Bau der als Hoden beschriebenen Lappenorgane des Aals” [“Observations on the Configuration and Finer Structure of the Lobed Organs in Eels Described as Testes”] can be found in *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe*, vol. 75 (1877), 419–431. Freud’s study was in response to Szymon Syrski’s book *Ueber die Reproductions-Organe der Aale* (1874).
- [105.](#) James Prosek, *Eels: An Exploration, from New Zealand to the Sargasso, of the World’s Most Amazing and Mysterious Fish* (New York: Harper, 2011), Chapter 1.
- [106.](#) Prosek, *Eels*, 5.
- [107.](#) Karine Rousseau, Salima Aroua and Sylvie Dufour, “Eel Secondary Metamorphosis: Silvering,” in Karine Rousseau and Sylvie Dufour, “Introduction to Fish First and Secondary Metamorphoses,” in *Metamorphosis in Fish*, edited by Sylvie Dufour, Karine Rousseau, and B. G. Kapoor, (Enfield, NH/Boca Raton, FL: CRC Press, 2012), 216–250.
- [108.](#) Prosek, *Eels*, 3.
- [109.](#) Hirohiko Y. Kagawa, Yasuhiro Sakurai, Ryohta Horiuchi, Yukinori Kazeto, Koichiro Gen, Hitoshi Imaizumi, and Yoshitsugu Masuda, “Mechanism of Oocyte Maturation and Ovulation and Its Application to Seed Production in the Japanese Eel,” *Fish Physiology and Biochemistry* 39, no. 1 (February 2013): 13–17, doi:10.1007/s10695-012-9607-3.
- [110.](#) Catherine Reef, *Sigmund Freud: Pioneer of the Mind* (New York: Clarion Books, 2001), 28; Prosek, *Eels*, 5.
- [111.](#) “Anguillidae,” *Wikipedia*, accessed on September 9, 2015, <http://en.wikipedia.org/wiki/Anguillidae>.
- [112.](#) “Eel life history,” *Wikipedia*, accessed on September 9, 2015, http://en.wikipedia.org/wiki/Eel_life_history#Past_studies_of_eels.
- [113.](#) Andrew J. H. Davey and Donald J. Jellyman, “Sex Determination in Freshwater Eels and Management Options for the Manipulation of Sex,” *Reviews in Fish Biology and Fisheries* 15, no. 1 (February 2005): 37–52. As the authors comment on page 48: “Eels are enigmatic animals and the factors that influence the onset and determination of sex in juveniles have proved difficult to pin down.” As they point out, see page 37: “Although heteromorphic sex chromosomes have been identified in some species, gender appears to be determined principally by environmental factors.”
- [114.](#) Friedrich-Wilhelm Tesch *The Eel*, edited by John E. Thorpe, 3rd ed. (Oxford: Blackwell Science, 2003). See page 43, where the authors comment: “An important and controversial issue from both a scientific and practical viewpoint is the question of sex determination. From results cited in previous sections it is obvious that microscopically recognizable ‘intermediate (intersexual) stages occur in eels. Thus the gonadal anlage passes through phases during which either male or female types could develop, and the direction of development may be influenced by environmental factors.”
- [115.](#) Tesch and Thorpe, *The Eel*, 44.
- [116.](#) “Fishes,” *Encyclopedia Britannica*, fifteenth edition (2002), vol. 19, 225–227.
- [117.](#) Prosek, *Eels*, 6; “Eel life history,” http://en.wikipedia.org/wiki/Eel_life_history.
- [118.](#) Prosek, *Eels*, Chapter 1; Tesch, *The Eel*, Chapter 2.
- [119.](#) Prosek, *Eels*, 3.
- [120.](#) David Righton and Mandy Roberts, “Eels and People in the United Kingdom,” in *Eels and Humans*, edited by

Katsumi Tsukamoto, and Mari Kuroki (Tokyo; New York: Springer, 2014), 1–12, 1.

[121.](#) Ibid., “Fishes,” *Encyclopedia Britannica*, fifteenth edition (2002), vol. 19, 225–227.

[122.](#) Righton and Roberts, “Eels and People in the United Kingdom, 1.

[123.](#) Ibid.

[124.](#) “Eel life history,” http://en.wikipedia.org/wiki/Eel_life_history.

[125.](#) Karine Rousseau and Sylvie Dufour, “Introduction to Fish First and Secondary Meta-morphoses,” in *Metamorphosis in Fish*, edited by Sylvie Dufour, Karine Rousseau, and B. G. Kapoor, 1–11, see page 9 for the term prepubertal maturity. The authors use the term “prepubertal” to describe the silver eel stage just prior to commencing their migration back to the Sargasso.

[126.](#) Tesch, *The Eel*, 169.

[127.](#) Ibid., 165–166.

[128.](#) Prosek, *Eels*, 3. As Prosek comments on page 3: “Wherever eels are born, they’re relentless in their efforts to return to their oceanic womb.” Surmounting beach walls is cited in Tesch, *The Eel*, 184.

[129.](#) Tesch, *The Eel*, 169.

[130.](#) Ibid., 24–27; Rousseau, Aroua and Dufour, “Eel Secondary Metamorphosis: Silvering,”

[131.](#) Ibid.; “Eel life history,” http://en.wikipedia.org/wiki/Eel_life_history.

[132.](#) Rousseau Aroua and Dufour, “Eel Secondary Metamorphosis: Silvering.”

[133.](#) Ibid.

[134.](#) Charles Darwin, *On the Origin of Species*, sixth edition (London, John Murray, 1869), 251.

[135.](#) Prosek, *Eels*, 9.

[136.](#) *Encyclopedia Britannica*, fifteenth edition (2002), vol. 19, 225, Figure 17.

[137.](#) Tim F. Flannery and Peter Schouten, *Astonishing Animals: Extraordinary Creatures and the Fantastic Worlds They Inhabit*, first American ed. (New York: Atlantic Monthly Press, 2004), 181.

[138.](#) Ibid., 161.

[139.](#) Ibid., 191.

[140.](#) Letter of Darwin to Alfred Russell Wallace, June 15, 1864. Text available at Darwin Correspondence Project, <http://www.darwinproject.ac.uk/entry-4535>.

[141.](#) Karl Ludwig von Bertalanffy, “Chance or Law,” in *Beyond Reductionism: New Perspectives in the Life Sciences*, edited by Arthur Koestler (London: Hutchinson, 1969), 65.

Chapter 10—Bridging Gaps: The Origin of Language

[1.](#) Ian Tattersall, *Becoming Human: Evolution and Human Uniqueness* (Orlando: Houghton Mifflin Harcourt, 1999), Chapter 1.

[2.](#) Ibid., Chapter 1.

[3.](#) 500,000 years ago, if Neanderthals and other archaic humans are members of our species. See the discussion below of the Neanderthals and Denisovans.

[4.](#) Alfred Russel Wallace, “The Limits of Nature Selection as Applied to Man,” in *Contributions to the Theory of Natural Selection*, second edition (New York: MacMillan, 1871), Chapter 10. This work is available online at <https://archive.org/details/contributionsto01wallgoog>.

[5.](#) Ibid., 336.

[6.](#) Ibid., 343.

7. Noam Chomsky, *The Science of Language: Interviews with James McGilvray* (New York: Cambridge University Press, 2012), 15.
8. “Neanderthal,” *Wikipedia*, accessed on September 9, 2015, <http://en.wikipedia.org/wiki/Neanderthal>; Paola Villa and Wil Roebroeks, “Neandertal Demise: An Archaeological Analysis of the Modern Human Superiority Complex,” *PLoS ONE* 9, no. 4 (April 30, 2014): e96424, doi:10.1371/journal.pone.0096424; Ruggero D’Anastasio, Stephen Wroe, Claudio Tuniz, Lucia Mancini, Deneb T. Cesana, Diego Dreossi, Mayoorendra Ravichandiran, Marie Attard, William C. H. Parr, Anne Agur, and Luigi Capasso, “Micro-Biomechanics of the Kebara 2 Hyoid and Its Implications for Speech in Neanderthals,” *PloS One* 8, no. 12 (2013): e82261, doi:10.1371/journal.pone.0082261.
9. Richard E. Green, Johannes Krause, Susan E. Ptak, Adrian W. Briggs, Michael T. Ronan, Jan F. Simons, Lei Du, Michael Egholm, Jonathan M. Rothberg, Maja Paunovic, and Svante Pääbo, “Analysis of One Million Base Pairs of Neanderthal DNA,” *Nature* 444, no. 7117 (November 16, 2006): 330–336, doi:10.1038/nature05336.
10. Svante Pääbo, *Neanderthal Man: In Search of Lost Genomes* (New York: Basic Books, 2014), 252–253.
11. “Neanderthal,” <http://en.wikipedia.org/wiki/Neanderthal>.
12. As Jared Diamond points out in *Guns, Germs, and Steel: The Fates of Human Societies* (New York: W. W. Norton, 1997), “The Tasmanians had one of the simplest material cultures of any people in the modern world... [They lacked] barbed spears, bone tools of any type, boomerangs, ground or polished stone tools, hafted stone tools, hooks, nets, pronged spears, traps, and the practices of catching and eating fish, sewing, and starting a fire.” (312)
13. Carl Safina, *Beyond Words: What Animals Think and Feel* (New York: Henry Holt and Company, 2015)
14. Chomsky, *The Science of Language*, 47; Marc D. Hauser, Charles Yang, Robert C. Berwick, Ian Tattersall, Michael J. Ryan, Jeffrey Watumull, Noam Chomsky, and Richard C. Lewontin, “The Mystery of Language Evolution,” *Frontiers in Psychology* 5, no. 401 (May 7, 2014): doi:10.3389/fpsyg.2014.00401.
15. Hauser et al., “The Mystery of Language Evolution.”
16. *Ibid.*, abstract.
17. “[Chomsky’s] approach thus remains radically opposed to that of Skinner or Piaget, for whom language is constructed solely through simple interaction with the environment. This latter, behaviourist model, in which the acquisition of language is nothing but a by-product of general cognitive development based on sensorimotor interaction with the world, would appear to have been abandoned as the result of Chomsky’s theories.” Bruno Dubuc, “Tool Module: Chomsky’s Universal Grammar,” *The Brain from Top to Bottom*, translated by Al Daigen, http://thebrain.mcgill.ca/flash/capsules/outil_rouge06.html.
18. Chomsky, *The Science of Language*, 5.
19. *Ibid.*, part 1.
20. Morten H. Christiansen and Nick Chater, “Language as Shaped by the Brain,” *Behavioral and Brain Sciences* 31, no. 05 (October 2008), doi:10.1017/S0140525X08004998. Bruno Dubuc, “Tool Module: Chomsky’s Universal Grammar,” http://thebrain.mcgill.ca/flash/capsules/outil_rouge06.html; Daniel L. Everett, *Language: The Cultural Tool* (New York: Vintage Books, 2012); Robert McCrum, “Daniel Everett: ‘There is no such thing as universal grammar,’” *The Guardian*, online, March 24, 2012, <http://www.theguardian.com/technology/2012/mar/25/daniel-everett-human-language-piraha>; Joshua K. Hartshorne, “How to Understand the Deep Structures of Language,” *Scientific American*, September 17, 2013, <http://www.scientificamerican.com/article/how-to-understand-the-deep-structures-of-language>.
21. Chomsky, *The Science of Language*, part 1.
22. Chomsky, *The Science of Language*, 13.
23. Steven Pinker, *The Language Instinct*, 1st ed. (New York: W. Morrow and Co., 1994), 373.
24. *Ibid.*, 319. Most medical interns will have witnessed the extraordinary specificity of functional loss in patients with CNS lesions.

- [25.](#) Ibid., 320–321.
- [26.](#) Ibid., 322.
- [27.](#) Dario Borghino, “Research at Stanford may lead to computers that understand humans,” *gizmag*, June 6, 2012, <http://www.gizmag.com/natural-language-processing/22811/>; “Home Page of the Loebner Prize in Artificial Intelligence: The First Turing Test,” April 27, 2015, <http://www.loebner.net/Prizef/loebner-prize.html>.
- [28.](#) Ilias Papathanasiou, Patrick Coppens, and Constantin Potagas, *Aphasia and Related Neurogenic Communication Disorders* (Burlington, MA: Jones & Bartlett Learning, 2013).
- [29.](#) Peter F. MacNeilage, *The Origin of Speech*, Studies in the Evolution of Language, vol. 10 (Oxford; New York: Oxford University Press, 2008), 3: “‘The possession of speech’, T. H. Huxley once remarked, ‘is the grand distinctive character of man’ (1871). And indeed it dwarfs most other evolutionary achievements.”
- [30.](#) Chomsky, *The Science of Language*, 13.
- [31.](#) Noam Chomsky, “Discussion of Putnam’s comments,” in *Language and Learning: The Debate between Jean Piaget and Noam Chomsky*, edited by M. Piattelli-Palmarini, 1st ed. (Cambridge MA: Harvard University Press, 1980), 310–324, see page 321.
- [32.](#) Noam Chomsky, *Language and Mind*, 3rd ed. (Cambridge; New York: Cambridge University Press, 2006), 85–86.
- [33.](#) Tattersall, *Becoming Human*, 189.
- [34.](#) Ibid., 230, emphasis added.
- [35.](#) Ibid.
- [36.](#) Stephen J. Gould, Paul McGarr, and Steven P. R. Rose, *The Richness of Life: The Essential Stephen Jay Gould* (New York: W. W. Norton, 2007), 153–154. The saltational emergentist strictly non-Darwinian model of origins (Chomsky, Tattersall, Gould) that I am defending here and throughout the book implies that the transitions are programmed into nature and arise in particular organism that were at particular moments in evolutionary history pre-adapted or prefigured for them to occur. But just because nature is prefigured for the leaps does not mean that the emergent leaps do not represent major discontinuities in the order of things, such as between a subhuman primate brain and the human brain; between a dumb ape and a talkative human.

The prefiguring of the primate brain for the emergent leap (which I assume was the case) does not necessarily imply that there was any continuity in linguistic competence between ape and man. Consider: liquid water and solid ice. Ice can only form from water [H₂O] and in that sense we may consider water as prefigured for the formation of ice but there is no continuity of forms between water and ice. Or consider oxygen [O] and hydrogen [H] and water [H₂O]. Water can only be formed by uniquely combining the two pre-existing material forms oxygen and hydrogen. But there is absolutely not the slightest continuity in the properties of O and H and H₂O.

Note also a crucial fact: Although these (ice and liquid water; O and H and H₂O) are hugely different material forms and the discontinuities are absolute, the triggers which initiates the dramatic phase transitions are essentially trivial—in one case merely cooling water from one to zero degrees, to get ice; in another case, merely the bringing hydrogen and oxygen into close proximity in a gaseous mixture which results in the explosive formation of water. In the case of the origin of language, just because the trigger that caused the leap to language might have been very minor does not mean that the gap was trivial or that there is no real discontinuity. The fact that the change was minor which triggered the self-organization of the primate brain into the new human configuration possessed of linguistic ability has no bearing on the potential enormity of the gap.

On any theory of human origins, we are clearly modified hominids. The fact is we do share a vast suit of homologs with our higher primate cousins, from menstruation to the vermiform appendix. Our unique biological attributes are additional “add ons” to a basic primate design, and I think it must be assumed that they could only have been instantiated in prefigured “primate matter.”
- [37.](#) Terrence W. Deacon, *The Symbolic Species: The Co-Evolution of Language and the Brain* (New York: W. W. Norton, 1998); Pinker, *The Language Instinct*.
- [38.](#) Chomsky, *The Science of Language*, 49.

39. David Premack, "Gavagai! Or the future of the animal language controversy," *Cognition* 19: 207–296, see pages 281–282.
40. Pinker, *The Language Instinct*.
41. Todd M. Preuss, "Human Brain Evolution: From Gene Discovery to Phenotype Discovery," *Proceedings of the National Academy of Sciences* 109, no. Supplement_1 (June 26, 2012): 10709–10716, doi:10.1073/pnas.1201894109; The difference may be greater than commonly claimed see J. Cohen, "Evolutionary Biology: Relative Differences: The Myth of 1%," *Science* 316, no. 5833 (June 7, 2007): 1836–1836, doi:10.1126/science.316.5833.1836.
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46. Ibid., 91.
47. Ibid.
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Chapter 11—Beyond Chance: *Natura Non Facit Saltum*

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Chapter 12—Fossils: Long-Term Non-Adaptive Trends

1. Stephen Jay Gould, *The Structure of Evolutionary Theory* [hereafter *SET*] (Cambridge, MA: Belknap Press [Harvard], 2002), 351–352: “The German zoologist Wilhelm Haacke devised the word “orthogenesis” in 1893; but the concept implicitly motivated the entire formalist tradition... The word literally means ‘straight (line) generation,’ but the term never bore a merely descriptive meaning, and all evolutionists understood the wider import. Orthogenesis denotes the claim that evolution proceeds along defined and restricted pathways because internal factors limit and bias variation into specified channels.”
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3. Leo Berg, *Nomogenesis* (Cambridge, MA: MIT Press, 1966), 149. See also Gould, *SET*, Chapter 5.
4. Thomas H. Huxley, "Mr. Darwin's Critics" (1871), in *Darwiniana: Essays*, edited by Asa Gray (New York: D. Appleton and Company, 1896), 181.
5. Gould, *SET*, 365.
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11. In the case of mammals and birds (as well as all other vertebrates and indeed all animal species) the diploid generation (the organism) is multi-cellular (in man consisting of some ten thousand billion cells) but the haploid generation consists only of single-celled gametes and is therefore always unicellular. However, in all land plants both the diploid and haploid phases are multi-cellular. The multi-cellular haploid phase is known as the gametophyte, and this provides nourishment and support for the early stages in the development of the diploid phase, known as the sporophyte, which in most plants forms the main body of the plant. So plants have two alternating multicellular generations.
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14. *Ibid.*, 121.
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16. *Ibid.*, 417; Dev Raj Khanna and P. R. Yadav, *Biology of Fishes* (New Delhi, India: Discovery Publishing House, 2004), 78.
17. Romer, *The Vertebrate Body*, 416–424.
18. *Ibid.*
19. Berg, *Nomogenesis*, 125.
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- [39.](#) Ibid.
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- [44.](#) Henry F. Osborn, “Darwin and Paleontology,” in *Fifty Years of Darwinism* (New York: H. Holt and Company, 1909), 223.
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Chapter 13—Typology Redux

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- [5.](#) Thomas Nagel, *Mind and Cosmos: Why the Materialist Neo-Darwinian Conception of Nature Is Almost Certainly False* (New York: Oxford, 2012), 126.
- [6.](#) Jonathan Lear, *Aristotle: The Desire to Understand* (New York: Cambridge University Press, 1988), 20.
- [7.](#) Ibid., 20, emphasis added.
- [8.](#) Paul Davies, *The Accidental Universe* (New York: Cambridge University Press, 1982); John D. Barrow and Frank Tipler, *The Anthropic Cosmological Principle* (New York: Oxford University Press, 1988); John Gribbin and Martin Rees, *Cosmic Coincidences: Dark Matter, Mankind, and Anthropic Cosmology* (Golden, CO: ReAnimus Press, 2015); Paul Davies, *The Cosmic Blueprint: New Discoveries in Nature’s Creative Ability to Order the Universe* (Philadelphia: Templeton Foundation Press, 2004).
- [9.](#) Davies, *The Accidental Universe*, vii.
- [10.](#) Fred Hoyle, “The Universe: Past and Present Reflections,” *Engineering and Science* (November, 1981), 8–12, 12.
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- [12.](#) Jes K. Jørgensen, Cecile Favre, Suzanne B. Bisschop, Tyler L. Bourke, Ewine F. van Dishoeck, and Markus

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14. Shawn D. Domagal-Goldman, Antígona Segura, Mark W. Claire, Tyler D. Robinson, and Victoria S. Meadows, "Abiotic Ozone And Oxygen in Atmospheres Similar to Prebiotic Earth," *The Astrophysical Journal* 792, no. 2 (August 20, 2014): 90, doi:10.1088/0004-637X/792/2/90. The existence of oxygen is also considered a necessity for complex life. See David C. Catling, Christopher R. Glein, Kevin J. Zahnle, and Christopher P. McKay, "Why O₂ Is Required by Complex Life on Habitable Planets and the Concept of Planetary 'Oxygenation Time,'" *Astrobiology* 5, no. 3 (June 2005): 415–438, doi:10.1089/ast.2005.5.415.
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16. Paul Davies, *The Fifth Miracle: The Search for the Origin and Meaning of Life* (New York: Simon & Schuster, 1999).
17. Lear, *Aristotle: The Desire to Understand*, 20.
18. John R. Platt, "Properties of Large Molecules That Go beyond the Properties of Their Chemical Subgroups," *Journal of Theoretical Biology* 1 (1961): 342–358; Philip Warren Anderson, "More Is Different," *Science* 177 (1972): 393–396; Robert B. Laughlin, David Pines, Joerg Schamlian, Branko P. Stojkovic, and Peter Wolynes, "The Middle Way," *Proceedings of the National Academy Sciences USA* 97 (2000): 32–37; Margaret Morrison, "Emergence, Reduction, and Theoretical Principles: Rethinking Fundamentalism," *Philosophy of Science* 73, no. 5 (2006): 876–887. In a previous article I wrote: "Physicists have pointed out that as the natural scale is ascended—from the microscopic domain (dealing with atomic and molecular properties of matter in the nanometer range) through the mesoscopic domain (dealing with the properties of condensed matter in the micrometer range; the domain of the cell) to the macroscopic domain (dealing with the properties of large masses of matter above the micrometer range; the domain of everyday objects)—new emergent laws and new principles of organization emerge... Because of the hierarchic organization of nature into distinct layers, each with its own unique laws, there is no possibility of ever achieving... the "constructionist" agenda... building the world from the bottom up, based only on laws and properties of matter at a subatomic level... As Anderson [Anderson, "More is different," 393] points out, at each level of complexity: 'entirely new properties appear and the understanding of new behaviours requires research which is... as fundamental in its nature as any other.'" See Michael J. Denton, Govindasamy Kumaramanickavel, and Michael Legge, "Cells as Irreducible Wholes: The Failure of Mechanism and the Possibility of an Organicist Revival," *Biology & Philosophy* 28, no. 1 (January 2013): 31–52, 36.
19. Note that in this section I am using the term *epigenetic* mainly (but not exclusively, see below) to denote *emergent biological order* (cellular and organismic) that arises in living matter through the process of self-organization and is *not specified in the genes*. However, the term "epigenetic" is often used in the medical field to refer to inherited traits that are not encoded in the DNA and environmental influences on gene expression.
20. Michael J. Denton, "The Types: A Persistent Structuralist Challenge to Darwinian Pan- Selectionism," *BIO-Complexity* 2013, no. 3 (August 19, 2013), 1–18, 8–9.

21. Lewis Wolpert and Julian H. Lewis, "Towards a Theory of Development," *Federation Proceedings* 34, no. 1 (January 1975): 14–20, abstract.
22. August Weismann, *The Evolution Theory* (Bristol, England: Edward Arnold, 1904). Text available through Internet Archive at https://archive.org/stream/evolutiontheory01weis_0#page/403/mode/2up (vol.1) and https://archive.org/stream/evolutiontheory01weis_0#page/403/mode/2up (vol. 2).
23. Ibid., vol. 1, 403–404. Weismann writes: "For the cell too is a *machine*, indeed a very complex one... But the *living machine* differs from other *machines* in that it constructs itself But whence comes... to keep to our metaphor the levers, wheels and cranks... in the making of the *organic machine*." [emphasis added]
24. Ibid., vol. 2, 307. Available at: <https://archive.org/stream/evolutiontheoryt02weisuoft#page/306/mode/2up>.
25. Ibid. Weismann writes: "[To some authors] the species appears, so to speak, as a vital crystallization... [or] as an equilibrium of living matter, which becomes displaced from time to time, and passes over into a new state of equilibrium... The species is thus something conditioned from within... just like a crystal."
26. Ibid., vol. 1, 335.
27. Marta Linde-Medina, "Adaptation or Exaptation? The Case of the Human Hand," *Journal of Biosciences* 36 (2011): 575–585, 580, doi:10.1007/s12038-011-9102-5.
28. Jacques Monod, *Chance and Necessity* (London: Collins, 1972).
29. Francis Crick, *Of Molecules and Men* (Amherst, NY: Prometheus Books, 2004).
30. James D. Watson and Andrew Berry, *DNA: The Secret of Life* (New York: Alfred A. Knopf, 2003).
31. Evelyn Fox Keller, *The Century of the Gene* (Cambridge, MA: Harvard University Press, 2000), 6.
32. Denton, Kumaramanickavel, and Legge, "Cells as Irreducible Wholes: The Failure of Mechanism and the Possibility of an Organicist Revival," 43. Also see Wilhelm Johannsen, "Some Remarks about Units in Heredity," *Hereditas* 4 (1923): 133–141; Edward Stuart Russell, *The Interpretation of Development and Heredity: A Study in Biological Method* (Oxford: Oxford University Press, 1930); Paul Weiss, "The Living System: Determinism Stratified," in *Beyond Reductionism: New Perspectives in the Life Sciences*, edited by Arthur Koestler and John R. Smythies (London: Hutchinson and Co, 1969), 3–55; H. Frederik Nijhout, "Metaphors and the Role of Genes in Development," *Bioessays* 12 (1990): 441–446; Richard C. Strohman, "Ancient Genomes, Wise Bodies, Unhealthy People: Limits of Genetic Thinking in Biological Medicine," *Perspectives in Biology and Medicine* 37, no. 1 (1993): 112–144; Keller, *The Century of the Gene*; Gabor Forgács and Stuart A. Newman, *The Biological Physics of the Developing Embryo* (New York: Cambridge University Press, 2005), introduction; Aristotle, *Parts of Animals*, translated by Arthur Leslie Peck (London: Heinemann, 1937), 109. As Jonathan Lear describes the forms (see *Aristotle: A Desire to Understand*, Chapter 2), Aristotle's forms are the building plan for the house plus the actions of the builders who actualize the plan as a house—natural causal agencies (substantial forms), which bring a particular organic form into being.
33. Nijhout, "Metaphors and the Role of Genes in Development," 441.
34. Russell, *The Interpretation Of Development And Heredity*, 25–30.
35. Keller, *Century of the Gene*, Chapter 2; Evelyn Fox Keller, *Making Sense of Life* (Cambridge, MA: Harvard University Press, 2002), Chapter 4.
36. Keller, *Making Sense of Life*, 136.
37. Denton, Kumaramanickavel, and Legge, "Cells as Irreducible Wholes: The Failure of Mechanism and the Possibility of an Organicist Revival," 43. For the internal references, see the original article.
38. Cited in Keller, *The Century of the Gene*, 54; Francis C. Crick, "On Protein Synthesis," *Symposia of the Society for Experimental Biology* 12 (1957): 138–163, 152
39. Denton, Kumaramanickavel, and Legge, "Cells as Irreducible Wholes: The Failure of Mechanism and the Possibility

of an Organicist Revival,” 44.

40. Thibaut Brunet, Adrien Bouclet, Padra Ahmadi, Démosthène Mitrossilis, Benjamin Driquez, Anne-Christine Brunet, Laurent Henry, et al., “Evolutionary Conservation of Early Mesoderm Specification by Mechanotransduction in Bilateria,” *Nature Communications* 4 (November 27, 2013): doi:10.1038/ncomms3821; Matthias Chiquet, Laurent Gelman, Roman Lutz, and Silke Maier, “From Mechanotransduction to Extracellular Matrix Gene Expression in Fibroblasts,” *Biochimica et Biophysica Acta–Molecular Cell Research* 1793, no. 5 (May 2009): 911–920, doi:10.1016/j.bbamcr.2009.01.012; María Elena Fernández-Sánchez, Sandrine Barbier, Joanne Whitehead, Gaëlle Béalle, et al., “Mechanical Induction of the Tumorigenic B-Catenin Pathway by Tumour Growth Pressure,” *Nature* 523 (May 11, 2015): 92–95, doi:10.1038/nature14329. See also the ongoing research project headed by Emmanuel Farge, entitled “Mechanics and Genetics of Embryonic and Tumoral Development,” *Physical Chemistry*, Institut Curie, <http://umr168.curie.fr/en/research-groups/mechanics-and-genetics-embryonic-and-tumoral-development/mechanics-and-genetics-embr>.
41. Ibid.
42. Denton, Kumaramanickavel, and Legge, “Cells as Irreducible Wholes: The Failure of Mechanism and the Possibility of an Organicist Revival,” 44. For the internal references, see the original article.
43. Jim Collins, cited in the *Nature* opinion column “Life after the synthetic cell,” *Nature* 465 (May 27, 2010): 422–424, page 424, doi:10.1038/465422a. “Although the Human Genome Project has expanded the parts list for cells, there is no instruction manual for putting them together to produce a living cell. It is like trying to assemble an operational jumbo jet from its parts list—impossible.”
44. I was a functionalist and ardent gene-centrist when I wrote *Evolution*, and it was to a degree my belief that *the secret of life was in the genes* that attracted me to the genome project; my research was focused for many years on the search for genes responsible for human genetic diseases.
45. Stuart A. Kauffman, *The Origins of Order: Self-Organization and Selection in Evolution* (New York: Oxford University Press, 1993).
46. Stuart A. Kauffman, *At Home in the Universe: The Search for Laws of Self-Organization and Complexity* (New York: Oxford University Press, 1996), 23; see also Chapter 4.
47. David J. Depew and Bruce H. Weber, *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection* (Cambridge, MA: MIT Press, 1996); Scott Camazine, Jean-Louis Deneubourg, Nigel R. Franks, James Sneyd, Guy Theraulaz, and Eric Bonabeau, *Self-Organization in Biological Systems* (Princeton: Princeton University Press, 2003); Thomas Surrey, François Nédélec, Stanislas Liebler, and Eric Karsenti, “Physical Properties Determining Self-Organization of Motors and Microtubules,” *Science* 292 (2001): 1167–1171; Timothy J. Mitchinson, “Self-Organization of Polymer–Motor Systems in the Cytoskeleton,” *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 336 (1992): 99–106; Ray Keller, Lance Davidson, and David Shook, “How We Are Shaped: The Biomechanics of Gastrulation,” *Differentiation* 7 (2003): 171–205; Stuart A. Newman, “Developmental Mechanisms: Putting Genes in Their Place,” *Bioscience* 27 (2002): 97–104; Nijhout, “Metaphors and the Role of Genes in Development”; Frederik Nijhout, “When Developmental Pathways Diverge,” *PNAS* 96 (1999): 5348–5350; Brian C. Goodwin, *How the Leopard Changed Its Spots* (New York: Charles Scribner, 1994), Chapters Four and Five; Tom Misteli, “The Concept of Self-Organization in Cellular Architecture,” *The Journal of Cell Biology* 155, no. 2 (2001): 181–185; Franklin M. Harold, *The Way of the Cell* (New York: Oxford University Press, 2002).
48. Kauffman, *At Home in the Universe*, 35; Roger Lewin, *Complexity* (New York: Macmillan, 1992), see Chapter 2 entitled “Beyond Order and Magic.”
49. Camazine et al., *Self-Organization in Biological Systems*, 87.
50. Self-organized complexity is not the only means to “emergent form.” Emergent epigenetic order also arises spontaneously as the hierarchy of organic order is ascended. Two cells have emergent chemical and physical properties not possessed by an individual cell. A thousand cells have emergent natural properties—viscoelastic and other—not possessed by two cells. One neuron cannot make a nerve circuit, while three neurons linked together can

make a simple circuit. Similarly, in the case of neurons, the properties that can be realized when ten billion neurons interact are surely qualitatively very different to those which can be realized with only one thousand. Inevitably, because of the hierarchic organization of nature into distinct layers, each with its own unique laws, newly emergent properties arise as the hierarchy is ascended. This applies to the inorganic as well as the organic realm. Biology is no less than physics a “multileveled” science. Discoveries are invariably empirical, and phenomena at each level, from cell biology to psychology, are simply irreducible to the level below. One very special case of emergence is the phenomenon of mind and consciousness. The enigmatic nature of mind and the profound challenge it poses to explanation in terms of reductive materialism and Darwinism were discussed recently in Thomas Nagel’s *Mind and Cosmos*.

51. Alan Turing, “The Chemical Basis of Morphogenesis,” *Philosophical Transactions of the Royal Society of London*, Series B, Biological Sciences 237, no. 641 (August 14, 1952): 37–72.
52. Christian B. Anfinsen, “Principles That Govern the Folding of Protein Chains,” *Science* 181 (1973): 223–230.
53. In cell biology it is universally acknowledged that self-organization plays a critical role and that the form of cells arises mainly from the self-organization of their constituents rather than by instruction from a detailed blueprint in the genome. The titles of recent papers capture something of the increasing importance of self-organization in cell biology: Misteli, “The Concept of Self-Organization in Cellular Architecture”; Eric Karsenti, “Self-Organisation Processes in Living Matter,” *Interdisciplinary Science Reviews* 32, no. 2 (2007): 163–175; Eric Karsenti, “Self-Organization in Cell Biology: A Brief History,” *Nature Reviews Molecular and Cell Biology* 9, no. 3 (2008): 255–262. As Karsenti explains in the 2008 article, self-organization concepts that were first developed in chemistry and physics and then applied to various morphogenetic problems in biology over the past century are now beginning to be applied to the organization of the living cell; there are no “simple linear chains of causal events that link genes to phenotypes.” Misteli comments: “The future of cell biology will be to understand the collective behavior of cellular structures at the molecular level... moving from analyzing single molecule behavior to studying the cell biological behavior of entire systems... The possible role of self-organization as a basic principle in cellular architecture might be just the beginning.”
54. Misteli, “The Concept of Self-Organization in Cellular Architecture,” 184.
55. Franklin M. Harold, “To Shape a Cell: An Inquiry into the Causes of Morphogenesis of Microorganisms,” *Microbiological Reviews* 54, no. 4 (December 1990): 381–431, 386.
56. Franklin M. Harold, “Molecules into Cells: Specifying Spatial Architecture,” *Micro-biology and Molecular Biology Reviews* 69, no. 4 (December 1, 2005): 544–564, 559, doi:10.1128/MMBR.69.4.544-564.2005, emphasis added.
57. Gerald H. W. Lim, Michael Wortis, and Ranjan Mukhopadhyay, “Stomatocyte-Discocyte-Echinocyte Sequence of the Human Red Blood Cell: Evidence for the Bilayer-Couple Hypothesis from Membrane Mechanics,” *Proceedings of the National Academy of Sciences* 99 (2002): 16766–16769, doi:10.1073/pnas.202617299.
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59. Lim et al., “Stomatocyte-Discocyte-Echinocyte Sequence of the Human Red Blood Cell.”
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61. Govindasamy Kumaramanickavel, Michael J. Denton, Michael Legge, “No evidence for a genetic blueprint: The case of the ‘complex’ mammalian photoreceptor,” *Indian Journal of Ophthalmology* 62 (2015): 48–49, 49.
62. Wolpert and Lewis, “Towards a Theory of Development.”
63. Keller, Davidson, and Shook, “How We Are Shaped,” *Differentiation* 71 (2003): 171–205, 171; Forgács and Newman, *Biological Physics of the Developing Embryo* (New York: Cambridge University Press, 2005).

64. Lance A. Davidson, Michelangelo von Dassow, and Jian Zhou, "Multi-Scale Mechanics from Molecules to Morphogenesis," *The International Journal of Biochemistry & Cell Biology* 41, no. 11 (November 2009): 2147–2162, 2147, doi:10.1016/j.biocel.2009.04.015.
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67. Suzan Mazur, "The Origin of Form Was Abrupt Not Gradual," *Archaeology*, Archaeological Institute of America, October 11, 2008, <http://www.archaeology.org/online/interviews/newman.html>.
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72. Ibid., 339. Early in cardiac development the straight heart tube deforms into a c-shaped tube that is normally curved towards the right side of the embryo.
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78. Michael J. Denton, "Protein Based Life As an Emergent Property of Matter: The Nature and Fitness of the Protein Folds," (a paper presented at the John Templeton Research Symposium, Biochemistry and Fine-Tuning, October 11–12, 2003, at the Harvard-Smithsonian Center for Astrophysics) in *Fitness of the Cosmos for Life: Biochemistry and Fine-Tuning*, edited by John D. Barrow et al. (Cambridge: Cambridge University Press, 2007), 256–279.
79. Ibid.
80. Ibid.
81. Daniel M. Weinreich, "Darwinian Evolution Can Follow Only Very Few Mutational Paths to Fitter Proteins," *Science* 312, no. 5770 (2006): 111–114, see page 113.
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87. Conrad Hal Waddington, *New Patterns in Genetics and Development* (New York: Columbia University Press, 1962), 102–112, 107. See also Figure 20.
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91. Karsenti, "Self-Organization Processes in Living Matter."
92. Eric Karsenti, "Self-Organization in Cell Biology: A Brief History"; Frederic Backouche, Lior Haviv, David Groswasser, and Anne Bernheim-Groswasser, "Active Gels: Dynamics of Patterning and Self-Organization," *Physical Biology* 3, no. 4 (December 4, 2006): 264–273, doi:10.1088/1478-3975/3/4/004.
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95. Ron Amundson, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo* (Cambridge: Cambridge University Press, 2005), 241.
96. Hans Driesch, *The Science and Philosophy of the Organism: The Gifford Lectures Delivered Before the University of Aberdeen in the Year 1907* (London: Adam and Charles Black, 1908).
97. Alejandro S. Alvarado and Panagiotis A. Tsonis, "Bridging the Regeneration Gap: Genetic Insights from Diverse Animal Models," *Nature Reviews Genetics* 7 (2006): 873–884. As the authors comment (p. 877) an adult newt "[C]an regenerate many organs, including limbs, the tail, spinal cord... the lens and retina, the jaws and the heart."
98. Armin Moczek, Karen E. Sears, Angelika Stollewerk, Patricia J. Wittkopp, Pamela Diggle, Ian Dworkin, Cristina Ledon-Rettig, et al., "The Significance and Scope of Evolutionary Developmental Biology: A Vision for the 21st Century," *Evolution & Development* 17, no. 3 (June 2015): 198–219, doi:10.1111/ede.12125. In their paper the authors comment: "Many may have expected that the molecular processes involved in axis determination in *Drosophila* are conserved at least within flies... and that early embryogenesis and vulva specification of *Caenorhabditis elegans* should be broadly conserved in nematodes... Yet drastic changes in development were indeed observed in both instances, in spite of common, homologous final morphologies... a phenomenon we now recognize as developmental system drift."
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100. Davis and Patel, "Short, Long, and Beyond"; Liu and Kaufman, "Short and Long Germ Segmentation"; Günter P. Wagner, "How Wide and How Deep Is the Divide between Population Genetics and Developmental Evolution?" *Biology & Philosophy* 22, no. 1 (2006): 145–153.
101. Denton, "The Types: A Persistent Structuralist Challenge to Darwinian Pan-Selectionism," 14. For the internal references, see the original article. (Note that one might cite the conversion from long to short or short to long as two further examples of transitions that can't be explained in terms of cumulative selection.)

- [102.](#) Liu and Kaufman, “Short and Long Germ Segmentation,” 629.
- [103.](#) Trip Lamb and David A. Beamer, “Digits Lost or Gained? Evidence for Pedal Evolution in the Dwarf Salamander Complex (*Eurycea*, Plethodontidae),” *PLoS ONE* 7, no. 5 (2012): e37544.
- [104.](#) Scott F. Gilbert, *Developmental Biology*, 9th ed. (Sunderland, MA: Sinauer Associates, 2010), Chapter 6. Text available at <http://10e.devbio.com/article.php?id=92>.
- [105.](#) Tanguy Chouard, “Darwin 200: Beneath the Surface,” *Nature* 456, no. 7220 (November 2008): 300–303, see p. 300.
- [106.](#) Wagner, “How Wide and How Deep Is the Divide between Population Genetics and Developmental Evolution?” 148. In *Evolution: A Theory in Crisis* (Maryland: Adler & Adler, 1986), Chapter 7, I cited Gavin de Beer’s monograph, *Homology: The Unsolved Problem* (Oxford: Oxford University Press, 1971), to argue that homology is not explained by assuming that homologous structures are inherited from a common ancestor. Nearly three decades later, I think de Beer’s comments and the thrust of Chapter 7 have been entirely vindicated.
- [107.](#) Wagner, “How Wide and How Deep Is the Divide between Population Genetics and Developmental Evolution?” 148, emphasis added. It was always apparent that the adaptations built upon the homologies—Owen’s adaptive masks (like the various vertebrate limbs built upon the underlying pentadactyl pattern)—are far more variable than the underlying homology itself. From the advances in developmental genetics it is now clear that in many instances the homologous patterns also *are more robust* than the underlying generative process and gene circuits responsible for their assembly during development. This is truly remarkable. There is variation *above* (the various adaptive forms built upon the homology in different species) and variation *below* (the variable generative processes by which the homologous pattern is derived in development in different species), while the homologous pattern itself remains invariant across the many lineages in which it is conserved.
- [108.](#) Amundson, *The Changing Role of the Embryo in Evolutionary Thought*, 8.
- [109.](#) Nicolaas Adrianus Rupke, *Richard Owen: Biology without Darwin* (Chicago: University of Chicago Press, 2009), Chapter 4.
- [110.](#) Marc Godinot, “The Variety of Attitudes among Palaeontologists Faced with Evolution (1840–1870),” *Spanish Journal of Palaeontology* 27, no. 2 (2012): 151.
- [111.](#) Rupke, *Richard Owen: Biology without Darwin*, Preface.
- [112.](#) Although the work reported by Stuart Newman in “Form and Function Remixed,” the 2014 paper cited above, comes close to demonstrating this.

Chapter 14—The Priority of the Paradigm

- [1.](#) See Thomas Kuhn, *The Structure of Scientific Revolutions*, 4th ed. (Chicago: The University of Chicago Press, 2012); Michael Denton, *Evolution: A Theory in Crisis* (Maryland: Adler & Adler, 1986), Chapter Fifteen.
- [2.](#) See discussion in Chapter 1, Section 1.1.
- [3.](#) For details, see Massimo Pigliucci and Gerd B. Müller, eds., *Evolution: The Extended Synthesis* (Cambridge, MA: MIT Press, 2010).
- [4.](#) Günter P. Wagner, *Homology, Genes, and Evolutionary Innovation* (Princeton: Princeton University Press, 2014), 8.
- [5.](#) Ronald Amundson, *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo* (Cambridge: Cambridge University Press, 2005).
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